SPECIES COEXISTENCE IN RESTORED GRASSLAND PLANT COMMUNITIES: TRAIT-BASED RECRUITMENT, NICHE-NEUTRAL ASSEMBLY, AND HETEROGENEOUS MANAGEMENT

By

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ABSTRACT

A core objective in the field of ecology is to understand mechanisms responsible for species coexistence. Recruitment is an essential process for coexistence in plant communities, and a greater understanding of recruitment dynamics could facilitate the restoration of degraded ecosystems. Despite the pressing need for restoration of the highly fragmented tallgrass prairie biome, few restorations approach the diversity of native remnant prairies. In this dissertation I examine multiple facets of recruitment in restored tallgrass prairies from a community ecology perspective, identifying multiple factors that influence the outcome of recruitment events with implications for enhancing the diversity of tallgrass restorations.

Despite heightened interest in stochastic dynamics among community ecologist, the influence of stochasticity on recruitment in restored plant communities has been poorly explored. In the first chapter, I hypothesized that increased propagule pressure would moderate stochastic recruitment and lead to greater predictability of sown species assemblages in grassland restorations, while also revealing divergent species compositions associated with prescribed disturbances. To examine these hypotheses, I conducted a field experiment in which a gradient of multi-species propagule pressure was applied to plots which had been subjected to prescribed disturbance regimes of varying intensities. I analyzed compositional dissimilarity among experimental plots to demonstrate that increased recruitment in response to propagule pressure and disturbance moderated stochastic structuring of sown plant communities. Furthermore, higher propagule pressure resulted in compositional divergence among disturbance treatments and increased the strength of affinities between species and a given treatment, indicating the presence of niche-based species-sorting dynamics.

A greater understanding of the relationship between plant traits and recruitment success in restored grasslands may facilitate the development of management practices that enhance the establishment of species which exhibit poor recruitment. In the second chapter, I compiled recruitment data for 190 native species from 54 experiments conducted throughout the tallgrass prairie region, and I quantified 10 traits for each species to examine the relationship between plant traits and recruitment. Analyses demonstrated that increased recruitment potential was associated with flowering during mid to late summer, long flowering duration, intermediate seed mass, intermediate height, and clonality. Recruitment potential is greatest when species exhibit multiple beneficial trait values, but can be severely limited by the expression of multiple disadvantageous traits.

The diversity of tallgrass prairie restorations is primarily constrained by the poor recruitment of many native forb species. Although multiple strategies have been proposed to enhance forb diversity in established species-poor restorations, the efficacy of these practices has not been rigorously compared with empirical data. In the third chapter, I conducted field experiments at three Midwestern research areas to examine the effects of multiple disturbance regimes on local species richness and the recruitment of native prairie forbs sown at each site. Native richness increased in response to sowing without disturbance, though disturbances increased light availability for arriving colonists and further enhanced recruitment. Analyses illustrated significant compositional differences among the native forb communities associated with disturbance treatments at each site, though no treatment resulted in decisively superior forb establishment. While the outcome of restorative interseeding practices is highly contingent upon localized site characteristics, my results indicate that the application of mosaic disturbance regimes within a single restoration site could maximize plant community diversity. In addition,

heterogeneous management may concurrently enhance faunal diversity by providing the structural heterogeneity required to meet the diverse habitat needs of grassland birds.

These dissertation chapters collectively demonstrate that species diversity and composition in restored grasslands is regulated by many factors that influence recruitment. These factors include propagule pressure, the form and severity of disturbance regimes, local environmental conditions of restoration sites, and the aggregate of traits expressed by sown species.

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GENERAL INTRODUCTION

Human land-use practices have drastically altered the composition of plant communities worldwide (Hooper et. al. 2005), contributing to an unprecedented mass extinction event and globally declining biodiversity (McCann 2000). Grasslands, which comprise upward of 40% of the terrestrial landscape (Briggs et al. 2005), are among the Earth's most imperiled ecosystems due to agricultural land-use conversion that has resulted in fragmentation and substantial losses of biodiversity and ecosystem function (Vitousek et al. 1997, Collins et al. 1998, Ceballos et al. 2010). The tallgrass prairie biome of North America covered approximately 162 million hectares prior to European settlement (Samson and Knopf 1994), forming a vast swath of continuous grassland spanning from Manitoba to Texas and eastward to Indiana (Packard and Mutel 1997). The most recent published estimates approximate that as little as 1% of the historical extent of native tallgrass prairie remains intact, which represents the largest decline of any major North American ecosystem (Samson and Knopf 1994). The loss of remnant tallgrass prairies has continued over the past decades, further reducing critical habitat for endangered and threatened species (Kindscher et al. 2005, Kindscher et al. 2009). Grassland insect species have declined due to rarity of host-plants (Reis et al. 2001, Vogel et al. 2007, Nemec and Bragg 2008), and grassland birds have experienced more precipitous declines than any other avian assemblage in North America (Sauer et al. 2008). Given that dispersal is necessary for stable local-scale coexistence of many species in meta-populations (Hanski 1999), isolated prairie remnants in a highly fragmented landscape are inadequate to support long-term persistence for many endemic species of the tallgrass fauna and flora (Herkert 1994, Maschinksi 2006). Accordingly, large-scale restorations of the tallgrass prairie are necessary to provide critical habitat for declining grassland species (Herkert et al. 2003, Schultz and Crone 2005, Olechnowski et al. 2009).

Tallgrass prairie is likely the biome with the longest history of ecological restoration (Mlot 1990), with well-documented restorations conducted at the University of Wisconsin arboretum as early as the 1930's (Cottam and Wilson 1966). In spite of this history and the tremendous need for restoration of this threatened ecosystem, restored prairies rarely approach the diversity of remnant prairies that serve as reference communities for assessing the relative success of restoration efforts (Kindscher and Tieszen 1998, Weber 1999, Sluis 2002, Lockwood and Samuels 2004, Martin et al. 2005, Polley et al. 2005). In order for applied restoration efforts to achieve greater diversity, the science of restoration must further incorporate current ecological knowledge and address the underlying mechanisms responsible for species coexistence and plant community response to restoration practice (Hobbs and Norton 1996, Palmer 1997, Young 2005, Temperton et al. 2004).

Given that a primary goal of community ecology is to determine how species co-exist, ecological restoration and community ecology are integrally linked, and synthesis of these fields promotes their mutual advancement. Ecologist have clearly recognized the potential restoration applications of fundamental issues in community ecology such as community assembly (Drake 1991, Young et al. 2001), assembly rules (Keddy and Weiher 1999, Temperton et al. 2004), alternative states (Suding et al. 2004), succession (Luken 1990, Packard 1994), disturbance (White and Jentsch 2004, MacDougall and Turkington 2007), and invasions (Seabloom and Van der Valk 2003, Biondini 2007). The underlying justification for applications of community ecology to restoration is obvious: while no ecological knowledge is required for environmental destruction, the reconstruction of degraded natural systems requires a thorough understanding of how ecological communities function (Bradshaw 1983). Conversely, ecological restoration may

serve as a litmus test for ecological theory so long as proper experimental designs and monitoring protocols are integrated into restoration projects.

Recruitment processes strongly influence species-coexistence in plant communities, and a greater understanding of factors which affect recruitment is critical for enhancing the diversity of degraded habitats. Recruitment refers to the process through which individuals immigrate into a community and successfully establish following arrival. Due to extreme fragmentation in the tallgrass prairie biome, restoration sites are often too isolated from potential source populations for colonization of many native species to occur naturally. Instead, seed of native tallgrass prairie species must commonly be dispersed artificially into restorations by sowing, which permits a unique framework for the examination of recruitment dynamics in plant communities. Competition/colonization tradeoffs, in which competitively superior species are locally absent due poor dispersal ability, are a key trait-based mechanism of coexistence in natural communities (Tilman 1994, Kneitel and Chase 2004). Sowing experiments can potentially counteract these tradeoffs by concurrently introducing propagules for multiple species with asymmetric competitive abilities, thus illuminating other factors that may determine the outcome of recruitment events when dispersal limitations are reduced.

This dissertation examines multiple facets of recruitment in plant communities through complimentary studies addressing fundamental issues in community ecology with implications for tallgrass prairie restoration. In the first chapter, I conduct a manipulative seed addition experiment to examine the role of propagule pressure (the density at which species are sown) in moderating compositional stochasticity of native species sown into plots subjected to varied disturbance regimes. The conceptual divergence between niche-based theories of coexistence (MacArthur 1958, Hutchinson 1959, Tilman 1982, Chesson 2000) and neutral theory (Bell 2000,

Hubbell 2001) has heightened awareness of the important role of stochasticity in regulating community dynamics (Tilman 2004, Gravel et al. 2006, Chase 2007). Immigration rates may determine the relative influence of stochastic and deterministic forces on structuring community compositions. Recruitment limitation is well documented in many natural communities (Turnbull et al. 2000, Myers and Harms 2009), and infrequent and stochastic recruitment may obscure the expression of competitive hierarchies among locally coexisting species and generate relatively stochastic patterns of community composition due to a relaxed intensity of interspecific interaction (Tilman 2004, Chase 2005). Accordingly, increasing the density of individuals available to a community may act to moderate the relative importance of stochastic forces for shaping species assemblages (Orrock and Fletcher 2005, Orrock and Watling 2010). Increased propagule pressure in conjunction with disturbance, which can free limited resources for arriving colonists, may enhance recruitment rates in local communities (Davis et al. 2000) and promote deterministic patterns of community composition (Tilman 2004).

Recent applications of permutational analysis (Anderson 2001, McArdle and Anderson 2001, Anderson et al. 2006; 2009) can utilize similarity indices to examine compositional differences among treatment groups and, furthermore, to analyze treatment effects on the compositional dissimilarity of within-group replicates, which provides a measure of stochasticity given the absence of environmental heterogeneity. By manipulating both propagule pressure and disturbance and employing these novel analytical approaches, I am able to examine the effect of recruitment density on the stochastic structuring of sown species assemblages and to examine whether high propagule pressure exposes niche-based species sorting dynamics associated with the unique environmental characteristics of specific disturbance regimes. A greater understanding of factors that influence the stochasticity of recruitment events has implications

for assessing the compositional predictability of communities created by restorative seeding and for selecting practices that will optimize diversity at various spatial scales.

In the second chapter, I have synthesized recruitment data from seed addition and restoration experiments conducted across the tallgrass prairie region in order to examine the relationship between plant traits and the recruitment success of native prairie species. Analyzing interactions between the traits expressed by species and ecological patterns and processes has emerged as an important means of addressing ecological questions (Cornelissen *et al*. 2003, Wright *et al*. 2004, Kleyer *et al*. 2008). Traits have been fundamental to interpretations of classical models of coexistence such as limiting similarity (Pacala and Tilman 1994, Weiher *et al*. 1998), niche partitioning (McGill *et al*. 2006, Violle and Jiang 2009), and competition/colonization tradeoffs (Levine and Rees 2002; Turnbull *et al*. 2005). Analysis of restoration studies permits a unique opportunity to examine relationships between plant traits and recruitment in isolation from the effects of dispersal. Accordingly, successful recruitment in restorations is expected to be indicated by traits associated with competitive ability, such as large seed mass (Rees *et al*. 1993, Leishman *et al*. 2000), tall height (Gaudet and Keddy 1995, Weiher *et al*. 1999, Bullock *et al*. 2001), and clonal growth (Olejniczak 2001, Cornelissen *et al*. 2003).

Because examining the generality of ecological patterns requires data synthesis from numerous studies encompassing a large geographic scale (McIntyre *et al*. 1999; Goldberg *et al*. 1999), I compiled data from 54 studies conducted throughout the tallgrass region in which native prairie species were sown and their recruitment was subsequently monitored. I then quantified 10 traits for each of the 190 native prairie species sown in the compiled studies and analyzed recruitment success in relation to trait characteristics. This approach facilitates the identification of persistent relationships between plant traits and recruitment that emerge in spite of substantial

environmental variation among grassland restoration sites. A greater understanding of the traits associated with species that persistently exhibit low or high recruitment rates will facilitate the development of practices for enhancing the diversity achieved through ecological restoration.

In the third chapter, I examine the effects of multiple disturbance regimes on the recruitment of prairie forbs sown into species-poor native grasslands at three Midwestern research areas and evaluate the potential for mosaic disturbance management to increase floral and structural heterogeneity at larger scales of restoration. While the dominant native warm-season grasses are easily established in prairie restorations, the low diversity of these restorations is attributed to the poor establishment and persistence of forb species (Schramm 1992, Weber 1999), which comprise the vast majority of species richness in remnant native communities (Weaver 1934, Collins et al. 1998). Forb establishment is thought to be inhibited by the competitive dominance of established warm-season grasses (Collins 1992, Copeland et al. 2002) and the reduced light availability caused by thatch accumulation of grasses (Tilman 1993, Knapp and Seastedt 1986, Facelli and Facelli 1993). As a result, disturbances may be necessary to increase the availability of light and other limiting resources for arriving forb propagules (Davis et al. 2000, Davis and Pelsor 2001). Though multiple disturbance practices have been suggested to facilitate forb colonization in established tallgrass restorations, I am unaware of any studies that have directly compared the effect of these disturbance regimes on the recruitment of native forb species.

I developed experimental sites in established warm-season grass plantings in Kansas and Missouri in order to experimentally compare the recruitment of native and exotic species in treatment units subjected to multiple contrasting disturbance regimes. I further evaluated whether a mosaic of different managed disturbances could be prescribed within large-scale restorations to effectively increase floral diversity. The assertion that biodiversity is greatest when disturbances

are applied across the landscape in a spatially and temporally heterogeneous fashion is a common principle in community ecology (Huston 1979), which has found substantial support from studies of prairie management (Howe 1994a, Davison & Kindscher 1999, Brudvig et al. 2007). The mosaic application of multiple forb enrichment strategies in established warm-season grasslands may also increase faunal diversity by concurrently providing habitat for species that are disturbance-dependent and disturbance-sensitive. Such novel management practices are needed to meet the diverse habitat requirements of declining grassland bird assemblages (Fuhlendorf et al. 2009), and represent an important advancement towards a more comprehensive approach to restoration. Collectively, these dissertation chapters apply principles of community ecology to interpret multiple facets of recruitment in restored grasslands, which has vital implications for the restoration and conservation of the tallgrass prairie landscape.

Chapter 1

Increased propagule pressure moderates stochastic recruitment

CHAPTER SUMMARY

Efforts to reconcile niche-based and neutral theories of coexistence have heightened interest in examining conditions that alter the relative influence of stochastic and deterministic forces on structuring ecological assemblages. Infrequent recruitment due to dispersal limitations and low resource availability is thought to impose a pivotal stochastic filter on the composition of natural communities. To determine the importance of propagule pressure and disturbance for mediating the stochasticity of recruitment, we conduct a seed addition experiment in which both factors were manipulated in an established low-diversity native grassland restoration. Analyses of the compositional dissimilarity of established sown species within and among treatment levels confirmed our hypotheses that enhanced recruitment in response to propagule pressure and disturbance would overwhelm stochastic filters on species composition and, furthermore, that greater propagule pressure would reveal species-sorting effects that produce divergent compositions associated with the specific conditions of each disturbance regime. Higher density of sown species may have increased within-treatment compositional similarity by concurrently intensifying interactions among colonists and the probability that species with asymmetric competitive abilities would be locally present. High propagule pressure magnified the divergence of species compositions among treatments and the strength of affinities between species and a given treatment, indicating the expression of species-sorting dynamics during initial recruitment. These findings provide evidence that ecological communities are structured by the collective influence of both niche-based and stochastic processes.

INTRODUCTION

Interpretation of mechanisms responsible for the diversity and composition of species assemblages is a fundamental objective of community ecology. Traditional niche-based explanations of coexistence have relied upon species trait differences that govern localized competitive interactions and niche-based trade-offs for explaining patterns of species composition and diversity at multiple spatial scales (Chesson 2000, Kneitel and Chase 2004). However, it has long been recognized that unpredictable and stochastic events also play an important role in structuring communities. The importance of stochasticity in community dynamics has been brought to the forefront in recent years with the development of neutral theory (Bell 2000, Hubbell 2001), which has been relatively successful in accounting for natural patterns of species abundance under the simplifying assumption of demographic and competitive equivalence among species. In neutral models, all dynamics reflect demographic stochasticity rather than the deterministic signature of niche relations. Predictions of neutral theory have given rise to a contentious dichotomy in the literature between neutral and niche-based perspectives, promoting many experimental tests and resulting in the publication of somewhat contradictory claims that the predictions of neutral theory are refuted (McGill 2003, Adler 2004, Turnbull *et al.* 2005, Harpole and Tilman 2006) or supported (Condit *et al.* 2000, Volkov *et al.* 2003, Allouche and Kadmon 2009) by empirical data.

While the unequivocal acceptance or rejection of neutral theory among ecologist is improbable, there is a growing consensus that productive advances towards understanding biodiversity and community structure may be achieved through a synthesis of niche-based and neutral perspectives (Chase 2003, Chave 2004, Tilman 2004, Chase 2005, Orrock and Fletcher 2005, Gravel *et al.* 2006, Holyoak and Loreau 2006, Leibold and McPeek 2006, Adler *et al.*

2007, Cadotte 2007, Chase 2007, Jabot *et al.* 2008, Vergnon *et al.* 2009, Orrock and Watling 2010). Although the critical assumption of neutrality (demographic and competitive equivalence among species) must be discarded to reconcile neutral and niche-based theories, other dynamics that are essential for neutral theory, such as stochasticity and dispersal limitation, play a vital role in synthetic perspectives (Gewin 2006). Stochastic is not synonymous with neutral, as systems where species are not demographically equivalent may also be highly stochastic in their behavior. Accordingly, one objective of synthetic approaches is to determine how community characteristics operate at various scales to moderate the relative importance of stochastic and deterministic (niche-based) forces in shaping species assemblages.

Trait variation among species can impose competitive inequalities, though the expression of this deterministic signature in a community may be obscured or potentially nullified by the stochastic nature of infrequent recruitment (Tilman 2004, Chase 2005). Seed addition experiments have often demonstrated that natural communities are not saturated and that local species richness is limited by recruitment (Turnbull *et al.* 2000, Myers and Harms 2009). Recruitment can be controlled by both local and regional processes that interact to structure communities (Zobel *et al.* 2001, Foster 2001, Moquet *et al.* 2004). A scarcity of suitable microsites for germination and seedling survival can constrain recruitment locally, while recruitment can also be limited by low immigration rates from the regional species pool (Loreau and Moquet 1999).

Interactions between factors influencing competition and dispersal may be adequate to create a continuum between niche-structured and stochastically-structured communities (Gravel *et al.* 2006). Davis *et al.* (2000) proposed that the susceptibility of communities to biological invasion is dependent upon fluctuations in resource availability caused by a decline in resource uptake by

resident vegetation following disturbance. For invasion to actually occur this fluctuation must coincide with the arrival of propagules from the regional species pool. The relationship between determinants of invasibility and the role of stochasticity in structuring communities is articulated by the stochastic niche hypothesis (Tilman 2004), which recognizes that species vary in traits associated with competitive ability but that successful recruitment is dependent upon the arrival of propagules and subsequent growth and survival of individuals through exploitation of resources not consumed by established members of the community. The inherent rarity and stochasticity of this colonization process can result in divergent (or variable) patterns of community assembly in which otherwise similar localities differ in species composition. It is predicted that any factor which counteracts recruitment limitation, such as the addition of large numbers of propagules and resource pulses caused by disturbance, may enhance diversity and permit the coexistence of a greater number of individuals in local communities (Tilman 2004).

Neutral theory's origins in population genetics (Kimura 1983) provide a conceptual context for the relationship between community size and the relative influence of stochasticity on community composition. Orrock and Watling (2010) used spatial models of competition to demonstrate that patterns of species composition among replicates are increasingly deterministic as the density of individuals in a community increases, whereas stochasticity in small populations may neutralize competitive differences among species. Just as genetic drift in small populations may override the potential role of natural selection in determining allele frequencies, ecological drift can negate the role of competitive inequalities in determining community composition (Orrock and Fletcher 2005). Accordingly, with increasing propagule pressure, community dynamics may shift from a paradigm of stochasticity to one of species-sorting, in

which community composition more strongly reflects the relative competitive abilities of species in response to local environmental conditions (Leibold *et al.* 2004).

Measures of compositional dissimilarity among patches with relatively homogenous environmental conditions can be employed to quantify the relative influence of stochasticity in local communities (Chase 2003). Given that dispersal limitation may isolate communities from a regional species pool (Stevens *et al.* 2004), increased propagule pressure through seed addition emulates greater meta-community connectivity and may overcome stochastic constraints on recruitment, as indicated by greater community similarity among environmentally similar patches (see Chase 2003, Table 1). Compositional similarity could be further increased by disturbances, which can increase resource availability for arriving propagules and improve the probability of successful recruitment (Davis *et al.* 2000, Tilman 2004).

To assess the relative effect of stochasticity on regulating species recruitment in plant communities, we conducted a seed addition experiment in which a gradient of propagule pressure is applied to low-diversity native grasslands subjected to disturbance regimes of varying severity. We first hypothesize that the composition of sown species will become less stochastic as propagule pressure and disturbance intensity increase. When recruitment of sown species is constrained by a low density of both propagules and disturbance induced microsites, the limited probability of a propagule of any given species arriving at a suitable site for establishment should negate niche differences and relegate patterns of recruitment to the uncertainties of a stochastic lottery. As propagule pressure and disturbance intensity increase, presumably increasing the availability of establishment micro-sites and limiting resources such as light and nutrients, greater proximity among colonists with asymmetric competitive abilities should lead to more similar assemblages of sown species. Secondarily, we hypothesize that increased propagule

pressure will promote species-sorting and increase differentiation between species compositions associated with each disturbance treatment, because greater recruitment density will reveal variation in competitive hierarchies associated with the environmental conditions generated by each disturbance regime.

METHODS

Study site and experimental procedure

We conducted this study at the Nelson Environmental Studies Area (University of Kansas) in northeastern Kansas (39°N, 91°W). We established the experiment within a 5.6 hectare native warm-season grass planting that was converted from agricultural production in 1957 and is dominated by big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). We selected a study location within the site that exhibited maximal homogeneity of vegetative composition, structure, topography, and soil conditions.

In mid-April 2005 we established 15 permanently marked 4 x 4 m plots separated by 3 m buffer strips. We randomly assigned plots to receive one of three disturbance treatments (n=5) prior to seed addition that were intended to create variation in light availability for germination and initial establishment: no disturbance (undisturbed), summer burning (summer burn), or broad-spectrum herbicide application followed by summer burning (herbicide). A 5% solution of broad-spectrum herbicide (glyphosate) was uniformly sprayed in early July 2005, which resulted in complete mortality of all resident vegetation prior to burning. Prescribed burns were conducted in mid-August 2005.

The 4 x 4 m plots consisted of a block of four 2 x 2 m subplots, each designated to be sown at one of four levels of propagule pressure (none, low, mid, high) with mixes comprised of equal numbers of seeds per species for 37 native prairie forbs (Table 1). All species are characteristic of the native tallgrass prairie flora, but were absent from the site prior to sowing. Seed mixes were designed so that each species was sown at an equivalent individual density of 0 (none), 16 (low), 42 (mid), or 110 (high) seeds per m^2. To account for variation in viability, we only purchased seeds from single source accessions with pure live seed (PLS) estimates. We weighed 100 seeds of each species to calculate average seed mass, then weighted that value by PLS estimates to create seed mixes with approximately equal numbers of viable propagules per species. Seeds were mixed with sawdust to facilitate uniform distribution and were hand-broadcast in late December 2005.

We established permanent $1m^2$ quadrats centered within each 2 x 2 m subplot in which we counted stems of all herbaceous species during mid-June each year from 2005 through 2008. Multiple stems of a given species were recorded as independent occurrences unless we could confirm without disturbing the soil that stems were from the same genet. We acquired current species nomenclature from the PLANTS Database (USDA, NRCS 2010).

Photosynthetically Active Radiation (PAR; μmol m-2s-1) was measured to determine the effect of disturbances on light availability and provide a non-destructive measure of biomass. We measured PAR in mid-July from 2005-2007 using a 0.8-m AccuPAR LP-80 ceptometer (Decagon Devices, Pullman, Washington, USA). For each 4 x 4 m plot we calculated four PAR interception values (one per subplot) based on paired measurements recorded at approximately 50 cm above the canopy and at the soil surface, inserting the ceptometer probe beneath the litter layer when necessary. All light measurements were recorded at midday under clear sky

conditions. Light penetration was expressed as the percentage of PAR above the canopy to reach the soil surface, while biomass is inversely approximated by percent PAR interception.

Statistical analyses

To examine inter-annual changes in canopy light penetration in response to disturbance treatments, we conducted repeated-measures analysis of variance (ANOVA) and completed *a posteriori* multiple comparisons among treatments within each sampling year using Tukey's HSD test. We used stem count data from the $1m^2$ quadrats within each subplot to calculate density, richness, and evenness (E calculated as $H'/\ln S$) of sown species, examining data from the final sampling period to provide the greatest approximation of long-term treatment effects on community composition. We then employed repeated-measures ANOVA for split-plot designs to examine the effect of propagule pressure and disturbance on richness, density, and evenness of sown species. The preceding analyses were conducted in SPSS 17.0 for Windows (2008). To account for the effect of stem density variation on species richness (Gotelli and Colwell 2001) in response to different propagule pressures, we conducted individual-based rarefaction, which estimates the richness that would have been found in a given treatment at lower density, using the null model software program EcoSim (Gotelli and Entsminger 2009).

We quantified dissimilarity among sampling quadrats by calculating a matrix of Bray-Curtis dissimilarity values based on relative abundance of sown species stem counts using PC-ORD (McCune and Mefford 1999). Bray-Curtis dissimilarity ranges from 0 to 1, with higher scores indicating that the communities under comparison have different species compositions and/or abundances, and lower scores indicating both a similar composition and abundance of species.

To visually portray variation in sown species composition and within-treatment compositional dissimilarity among treatments across each level of propagule pressure and disturbance we performed Nonmetric Multidimensional Scaling (NMDS) in PC-ORD with 500 iterations of stem count relative abundance data using Bray-Curtis dissimilarity. To statistically evaluate differences in community composition among groups we performed Permutational Analysis of Variance (PERMANOVA) using the statistical package PERMANOVA+ for PRIMER 6 (Anderson *et al.* 2006) based on the methods of Anderson (2001) and McArdle & Anderson (2001), with P values for the test statistic (pseudo F value) based on 9,999 permutations of our similarity matrix. We first performed split-plot PERMANOVA to examine main effects and interactions of disturbance and propagule pressure, and then conducted one-way analyses to examine the effect of disturbance at each level of propagule pressure separately.

To test for differences of within-treatment dissimilarity (a measure of stochasticity) in response to propagule pressure and disturbance, we performed Permutational Analysis of Multivariate Dispersions (PERMDISP; Anderson 2006) using a freely available FORTRAN program (Anderson 2004). As above, P values were calculated using 9,999 randomly generated permutations of our Bray-Curtis dissimilarity matrix. We performed factorial PERMDISP to examine effects of propagule pressure, disturbance, and their interaction across all groups, and secondly we performed one-way PERMDISP to examine the effect of disturbance at each level of propagule pressure. While we realize that a factorial test does not account for the spatial non-independence of the split-plot factor in a split-plot design, we are unaware of any available program that performs split-plot designs for PERMDISP. Furthermore, we recognize the confounding possibility inherent to any field experiment that compositional dissimilarity among plots may be affected by unmeasured dimensions of environmental heterogeneity, but we have

no reason to suspect that the magnitude of such small-scale heterogeneity would vary among treatment groups given the random delineation of plots within a site selected for maximal homogeneity of environmental conditions.

Lastly, to identify sown species that underlie compositional differences among disturbance treatments at different levels of propagule pressure, we performed Indicator Species Analysis (ISA; Dufrene & Legendre 1997) in PC-ORD. For each species, ISA assigns an indicator value (*IV*) for each disturbance treatment that can range from 0-100% of perfect indication, based on species presence and stem density. Significance of the observed maximum *IV* with respect to treatment was calculated for each species using a Monte Carlo test with 9,999 iterations.

RESULTS

The undisturbed, summer burn, and herbicide treatments generated the desired variation in light availability, as illustrated by highly significant differences in post-treatment canopy light penetration for 2006 ($F= 44.6_{2,12}$ $p < 0.001$) compared to similar pre-treatment values for 2005 ($F= 0.5_{2,12}$ $p = 0.6$; Fig 1). In 2007, PAR was still significantly different among disturbance treatments ($F= 23.6_{2,12}$ $p < 0.001$) and remained elevated in response to herbicide application, but was no longer significantly higher in summer burned plots than in the undisturbed plots (Fig 1).

Increased propagule pressure had a highly significant ($p < 0.001$) positive effect on sown species richness (Table 2; Fig 2a), while the effect of disturbance was slightly non-significant ($p = 0.06$). However, this elevated richness appears to be a sampling effect caused by substantial stem density variation, since individual-based rarefaction indicates that once differences in

density are accounted for rarefied species richness does not significantly ($p < 0.05$) differ among levels of propagule pressure. Stem density of sown species demonstrated a significant ($p < 0.001$) positive response to propagule pressure, disturbance, and propagule x disturbance interactions (Table 2; Fig 2b). Significant effects of propagule pressure ($p = 0.005$) and propagule x disturbance interaction ($p = 0.001$) on sown species evenness (Table 2) are illustrated by an inconsistent response to disturbance at no and low propagule pressure, with declining evenness in response to disturbance at greater propagule pressures (Fig 2c).

Permutational Analysis of Multivariate Dispersions (PERMDISP) demonstrated significantly increased within-group compositional similarity of sown species (Table 2; Fig. 2d) in response to the main effects of increased propagule pressure ($F= 52.3_{3,48}$ $p < 0.001$) and disturbance ($F= 21.6_{2,48}$ $p < 0.001$). Increased propagule pressure caused replicates to aggregate more densely in NMDS ordination space across all disturbance levels (Fig 3), thus depicting greater compositional similarity. Although a propagule x disturbance interaction was not significant ($F= 1.2_{6,48}$ $p = 0.33$), several lines of evidence suggest that an ecological interaction occurred even if small sample sizes prohibited the detection of a significant statistical interaction. When factorial PERMDISP was conducted using a matrix of incidence based Jaccard similarity coefficients, thus ascribing equal weight to common and uncommon species, the interaction term was significant ($F= 2.7_{6,48}$ $p < 0.025$), and the significance of propagule pressure ($F= 51.7_{3,48}$ $p < 0.001$) and disturbance ($F= 20.1_{2,48}$ $p < 0.001$) was nearly unchanged relative to the abundance-based analysis (Table 2). Furthermore, evidence of an interaction is provided by examination of NMDS plots (Fig 3a-c), which illustrate that the effect of propagule pressure on compositional similarity became more pronounced as the severity of disturbance declined. The effect of disturbance on compositional similarity also diminished as propagule pressure increased and was

not actually significant at high propagule pressure (Fig 3d-f), suggesting that high propagule pressure alone could reduce stochastic recruitment even in the absence of disturbance.

While propagule pressure was the strongest determinant of compositional similarity within groups, pseudo F-values generated by split-plot PERMANOVA (Table 2) demonstrated that disturbance ($F= 5.3_{2,12}$ $p < 0.001$) had a greater effect than propagule pressure ($F= 3.6_{3,36}$ $p < 0.001$) on sown species composition differences among groups, but that propagule x disturbance interactions were not significant ($F= 1.0_{6,36}$ $p = 0.51$). As in the previous analyses, it appears that this lack of a significant statistical interaction may be a consequence of insufficient sample size, since other evidence suggests that an ecological interaction between propagule pressure and disturbance is present. Split-plot PERMANOVA based on coefficients of Jaccard similarity (Table 2) yielded an interaction that was only slightly non-significant ($F= 1.3_{6,36}$ $p = 0.06$), while both disturbance ($F= 4.5_{2,12}$ $p < 0.001$) and propagule pressure ($F= 3.1_{3,36}$ $p < 0.001$) remained significant. Consideration of one-way PERMANOVAs based on Bray-Curtis dissimilarity within each propagule pressure level (Table 2) demonstrated that differences in the composition of sown species among disturbance levels became markedly more significant with increased propagule pressure, as further illustrated by NMDS plots (Fig 3d-f). Furthermore, pairwise comparisons generated by PERMANOVA reveal that only the undisturbed and herbicide treatments were significantly different from one another at low propagule pressure, the undisturbed treatment was significantly different from both the summer burn and herbicide treatments at mid propagule pressure, and all three disturbance treatments had significantly different sown species compositions at high propagule pressure (Fig 3d-f, $p < 0.05$).

Further evidence of species sorting among disturbance treatments in response to increased propagule pressure is provided by Indicator Species Analysis (Table 1). At high propagule

pressure, the undisturbed and herbicide treatments were each associated with five significant indicator species (Undisturbed: *Monarda fistulosa, Penstemon digitalis, Polytaenia nuttallii, Vernonia baldwinii, Zizia aurea;* Herbicide: *Dalea purpurea, Oligoneuron rigidum, Salvia azurea, Solidago nemoralis, Symphyotrichum novae-angliae*) three of which remained as significant indicators of these two disturbance extremities at mid propagule pressure, while there were no significant indicator species for either treatment at low or no propagule pressure (Table 1). *Echinacea pallida* was a consistently significant indicator of the summer burning treatment at low, mid, and high propagule pressures, but there were no significant affinities between sown species and disturbances in the absence of seed addition.

DISCUSSION

Our analysis offers considerable evidence consistent with the hypothesis that the composition of sown species would become less stochastic and more predictable with greater propagule pressure and disturbance. The relative effect of stochasticity on recruitment appears to be strongly influenced by the number of individuals that successfully establish in a local community, which in turn is a function of propagule pressure and disturbance. Our empirical findings are consistent with models demonstrating that the relative importance of stochasticity is inversely related to community size and density (Gravel *et al.* 2006, Orrock and Watling 2010). As the number of individuals within a community of finite scale increases, both the intensity of competitive interactions and the likelihood that superior competitors are locally present concurrently increase. Low density of individuals caused by poor recruitment can allow inferior competitors

to “win by forfeit” and impede competitive asymmetries from structuring species compositions (Hurtt and Pacala 1995). Accordingly, dispersal limitation is thought to be a pivotal mechanism underlying the role of stochasticity in natural communities (Hubell 2001, Chase 2003, Stevens *et al.* 2004, Tilman 2004, Gravel 2006).

Competition/colonization tradeoffs, in which superior competitors are locally absent due to poor dispersal ability, are a key trait-based mechanism of coexistence (Tilman 1994, Kneitel and Chase 2004). Seed addition experiments such as ours can potentially counteract these tradeoffs by assuring that propagules of species with asymmetric competitive abilities are present at equivalent frequencies. Our experiment suggests that, when increased propagule pressure successfully enhances recruitment, intensified intraspecific interactions can expose competitive hierarchies and promote compositional similarity among environmentally similar communities. Local diversity should increase with recruitment pressure until a threshold is attained; beyond which greater density of individuals may decrease local diversity as the species best suited for successfully colonizing local habitats exclude less adept species (Moquet and Loreau 2002, Chase 2003). Although the sown species analyzed in this study had persisted into their third growing season, it would be presumptuous to contend that the composition of these experimental communities has reached a stable equilibrium. While richness of sown species did not decline in response to density over the duration of this experiment, declining evenness with increased density at mid to high propagule pressure (Fig 2) may be a precursor of decreased richness over longer temporal scales. This further suggests that compositional similarity among local communities may constrain diversity at the meta-community level (Chase 2003).

Rarefaction demonstrated that enhanced richness of sown species in response to high propagule pressure was a sampling effect that resulted from substantial increases in stem density.

While rarefaction is often necessary to account for variability in sampling effort or sampling area between communities, the absence of these inequalities in this study suggests that differences in stem density reflect ecologically meaningful responses to propagule and disturbance treatments (Gotelli and Colwell 2001). In light of the considerable compositional dissimilarity exhibited at low propagule pressures, these results imply that species richness at different levels of propagule pressure would be equivalent given a sufficiently large sampling area, despite persistently disparate stem densities. As the total stem density of sown species declines, a limited sampling area will yield lower species richness purely due to chance (Stevens and Carson 1999), which is congruent with patterns of increasingly stochastic recruitment as propagule pressure declines.

While density provides a simple means of interpreting the relative influence of stochastic processes on structuring patterns of recruitment (Orrock and Fletcher 2005, Orrock and Watling 2010), further interpretation requires consideration of the local and regional dynamics that determine the density of recruitment events (Chase 2003; 2005, Tilman 2004). Successful colonization events are dependent upon an increase in resource availability concurrent with the arrival of propagules (Davis *et al.* 2000, Tilman 2004), and previous studies have demonstrated that resource limitations in highly productive communities can negate the ability of seed addition to enhance recruitment (Foster 2001, Stevens *et al.* 2004). In our experiment, propagule pressure was the most significant determinant of stem density and increased compositional similarity even in the absence of disturbance, suggesting that limited propagule pressure, rather than productivity and resource consumption of resident vegetation, is the primary determinant of stochastic constraints on recruitment in this community (Foster 2001, Tilman 2004). However, more severe disturbance did augment the density of sown species at each propagule pressure level, indicating

that both local (microsite availability) and regional (dispersal) factors affect the outcome of colonization events (Moquet *et al.* 2004).

Increased disturbance intensity caused a fluctuation in available light and created suitable microsites for sown propagules (Fig 1). Light availability in grasslands is often suppressed by thatch accumulation, and other experiments have found that, as in this study, colonization success declines with reduced light (Tilman 1993, David and Pelsor 2001). Light availability can be a greater constraint than nutrient availability on species establishment in restored prairies (Camill *et al.* 2004), and may be an important limiting resource in disturbance dependent grasslands (MacDougall and Turkington 2007). In response to summer burning, light penetration to the soil surface was enhanced for only one growing season before returning to approximate pre-treatment levels, demonstrating that even short-term resource fluctuations can increase community invasibility (Davis and Pelsor 2001). In addition to altering light, prescribed fires can also produce temporary nutrient fluxes (Wan *et al.* 2001), which may have further facilitated species establishment. Application of broad-spectrum herbicide created a more enduring change in light availability and should have increased access for arriving propagules to soil resources that would have been consumed by resident individuals if not for their complete mortality. That this severe disturbance further increased compositional similarity following seed addition provides an extreme example of Tilman's (2004) assertion that resource consumption by resident vegetation creates a stochastic filter on recruitment.

Our analyses also support the hypothesis that increased propagule pressure promotes species-sorting dynamics, leading to increased differentiation between the compositions of sown species associated with each disturbance treatment. Although our initial analyses did not demonstrate a significant effect of an interaction between propagule pressure and disturbance intensity on

abundance-based compositional differences among groups, we believe there are compelling reasons to believe that an ecological interaction is present even if statistically muted by a limited sample size. Justification for this assertion is provided by incidence based analyses of compositional differences among groups, both statistical and visual evidence of amplified abundance-based compositional differences among disturbance treatments in response to increasing propagule pressure (Fig 3. d-f), and also increased affinities between sown species and disturbance treatments in response to increasing propagule pressure (Table 1) .

A species-sorting paradigm asserts that local community compositions are dependent upon interactions between traits and environmental conditions that determine relative competitive abilities among species (Leibold *et al.* 2004). Reconciliation of niche and neutral processes accepts that such interactions can shape communities, but that the stochasticity of infrequent recruitment prevents colonization by the species that are best suited to the local environment (Tilman 2004, Jabot *et al.* 2008). In other words, the expression of underlying habitat-specific competitive hierarchies is contingent upon high immigration rates (Loreau and Moquet 1999). While patterns of greater compositional stochasticity in response to dispersal limitation (low propagule pressure) are consistent with neutral theory, evidence of species-sorting among disturbance treatments is inconsistent with the neutral assumption of ecological equivalence. We found that high propagule pressure revealed differentiation among the community compositions associated with unique disturbance regimes (Figure 3f), and increased the significance and consistency of associations between particular sown species and the environmental conditions of each disturbance at the time of colonization (Table 1). These findings are congruent with models of Orrock and Watling (2010), which concluded that increased density in response to propagule pressure can shift control of community dynamics from neutral to niche-based paradigms.

Disturbance can create harsh environmental filters that yield deterministic assemblages by restricting the number of species that can withstand local conditions (Chase 2007). Increased propagule pressure may clarify the role of post-dispersal environmental filters on determining community structure (Jabot *et al.* 2008). Our results suggest that disturbances altered competitive hierarchies among sown species (Suding and Goldberg 2001) rather than implementing rigid abiotic filters. If rigid abiotic filters were governing community composition, then divergent assemblages associated with each disturbance regime should be well defined even at low propagule pressure (Fig 3d), because certain species would be strictly incompatible with the abiotic conditions induced by a given disturbance. Rather, our data indicate that high propagule pressure was necessary to reveal the disparate competitive hierarchies associated with successful colonization under the conditions generated by each disturbance regime.

Understanding the influence of propagule pressure and disturbance on the relative stochasticity of recruitment events could have applied implications for ecological restoration. Greater compositional similarity at small spatial scales may decrease diversity at larger scales because low β-diversity among homogenous patches limits α-diversity (Chase 2003), indicating that increased competitive interactions in response to excessive propagule pressure could limit restoration of landscape scale diversity in the absence of environmental heterogeneity. In contrast, species-sorting patterns suggest that both diversity and within-patch predictability of community composition in large-scale restorations may be maximized when heterogeneous disturbances are prescribed concurrently with high propagule pressure.

CONCLUSIONS

This experiment demonstrates that stochastic structuring of species assemblages generated by seed addition can be moderated by increased propagule pressure, producing similar compositions among local communities in the absence of environmental heterogeneity. In addition, sufficiently high recruitment rates can overwhelm stochastic filters to reveal evidence of species-sorting, as illustrated by divergence among the species compositions associated with specific disturbances. Experimental manipulation of dispersal rates and disturbance intensity can be a useful approach to expose mechanisms that may operate more subtly to influence stochasticity in natural communities. We suggest that our findings provide further support for the emergent perspective that both niche-based and neutral forces collectively structure ecological communities.

Table 1 The 37 native forb species sown in this experiment and results of Indicator Species Analysis. Group indicates the disturbance treatment in which a species exhibited maximal abundance. Indicator Values (IV) are measures (0 to 100) of the fidelity of species occurrence with a particular group. Bold typeface designates significant indicator species ($P < 0.05$), as determined by Monte Carlo tests.

	High			Mid			Low		
Species	**Group**	**IV**	***P***	**Group**	**IV**	***P***	**Group**	**IV**	***P***
Achillea millefolium	-	-	-	-	-	-	-	-	-
Amorpha canescens	-	-	-	Undisturb	20	1.000	-	-	-
Asclepias syriaca	-	-	-	-	-	-	-	-	-
Asclepias tuberosa	-	-	-	-	-	-	-	-	-
Baptisia alba	Undisturb	47	0.136	Undisturb	47	0.384	Undisturb	62	0.202
Chamaecrista fasciculata	Undisturb	30	0.519	SumBurn	23	0.887	SumBurn	19	0.728
Coreopsis palmata	SumBurn	48	0.121	SumBurn	42	0.405	SumBurn	34	0.595
Dalea candida	SumBurn	10	1.000	-	-	-	-	-	-
Dalea purpurea	**Herbicide**	**71**	**0.020**	Herbicide	20	1.000	-	-	-
Echinacea pallida	**SumBurn**	**63**	**0.002**	**SumBurn**	**49**	**0.067**	**SumBurn**	**78**	**0.002**
Eryngium yuccifolium	Undisturb	41	0.426	Undisturb	26	0.712	Undisturb	10	1.000
Helianthus mollis	Herbicide	37	0.737	Undisturb	36	0.829	Herbicide	38	0.604
Heliopsis helianthoides	Undisturb	39	0.641	SumBurn	30	0.819	SumBurn	41	0.288
Heuchera richardsonii	-	-	-	-	-	-	-	-	-
Lespedeza capitata	SumBurn	47	0.144	SumBurn	21	0.453	-	-	-
Lespedeza virginica	SumBurn	27	0.811	SumBurn	40	0.280	SumBurn	17	0.722
Liatris aspera	SumBurn	20	0.938	Herbicide	21	0.872	Undisturb	10	1.000
Liatris pycnostachya	Undisturb	27	0.506	Herbicide	20	1.000	SumBurn	20	1.000
Mimosa quadrivalvis	Undisturb	33	0.783	SumBurn	27	0.477	Undisturb	10	1.000
Monarda fistulosa	**Undisturb**	**71**	**0.001**	Undisturb	60	0.120	Undisturb	33	0.334
Oligoneuron rigidum	**Herbicide**	**78**	**0.005**	Herbicide	68	0.033	Herbicide	40	0.287
Penstemon digitalis	**Undisturb**	**86**	**0.001**	**Undisturb**	**70**	**0.014**	Undisturb	55	0.124
Polytaenia nuttallii	**Undisturb**	**76**	**0.011**	Undisturb	36	0.297	Undisturb	40	0.280
Ratibida pinnata	Herbicide	44	0.390	SumBurn	43	0.295	Herbicide	49	0.105
Rudbeckia hirta	Undisturb	34	0.868	Undisturb	38	0.661	Herbicide	52	0.110
Rudbeckia subtomentosa	Herbicide	28	0.495	Herbicide	60	0.072	Herbicide	40	0.286
Salvia azurea	**Herbicide**	**51**	**0.021**	**Herbicide**	**56**	**0.021**	Herbicide	45	0.185
Solidago nemoralis	**Herbicide**	**68**	**0.021**	Herbicide	52	0.133	SumBurn	26	0.401
Solidago speciosa	Herbicide	24	0.730	Herbicide	18	0.728	Herbicide	20	1.000
Symphyotrichum laeve	-	-	-	-	-	-	-	-	-
Symphyotrichum novae-angliae	**Herbicide**	**75**	**0.001**	**Herbicide**	**70**	**0.006**	Herbicide	53	0.082
Symphyotrichum oolentangiense	-	-	-	-	-	-	-	-	-
Verbena hastata	-	-	-	-	-	-	-	-	-
Verbena stricta	Herbicide	29	0.495	SumBurn	20	1.000	Undisturb	11	1.000
Vernonia baldwinii	**Undisturb**	**57**	**0.031**	Undisturb	22	0.850	Undisturb	13	1.000
Veronicastrum virginicum	-	-	-	-	-	-	-	-	-
Zizia aurea	**Undisturb**	**69**	**0.009**	**Undisturb**	**66**	**0.042**	Undisturb	9	0.942

Table 2 Results of ANOVA, PERMANOVA, and PERMDISP tests for effects of propagule, treatment, and site x treatment intereactions. One-way analyses test for effects of disturbance within levels of propagule pressure.

Response Variable	Analysis	Propagule Pressure	Disturbance	Propagule x Disturbance
Richness	split-polt ANOVA	$F = 116.2_{3,36}$ $p < 0.001$	$F = 3.6_{2,12}$ $p = 0.06$	$F = 1.6_{6,36}$ $p = 0.18$
Stem Density	split-polt ANOVA	$F = 116.8_{3,36}$ $p < 0.001$	$F = 24.8_{2,12}$ $p < 0.001$	$F = 5.9_{6,36}$ $p < 0.001$
Evenness	split-polt ANOVA	$F = 5.2_{3,36}$ $p = 0.005$	$F = 2.1_{2,12}$ $p = 0.16$	$F = 5.1_{6,36}$ $p = 0.001$
Species Composition	split-plot PERMANOVA (*BC*)	$F = 3.6_{3,36}$ $p < 0.001$	$F = 5.3_{2,12}$ $p < 0.001$	$F = 1.0_{6,36}$ $p = 0.51$
Species Composition	split-plot PERMANOVA (*J*)	$F = 3.1_{3,36}$ $p < 0.001$	$F = 4.5_{2,12}$ $p < 0.001$	$F = 1.3_{6,36}$ $p = 0.06$
Species Composition	one-way PERMANOVA (*BC*)	N/A (Low propagule only)	$F = 1.8_{3,16}$ $p = 0.035$	N/A
Species Composition	one-way PERMANOVA (*BC*)	N/A (Mid propagule only)	$F = 3.3_{3,16}$ $p = 0.002$	N/A
Species Composition	one-way PERMANOVA (*BC*)	N/A (High propagule only)	$F = 6.0_{3,16}$ $p < 0.001$	N/A
Compositional Dissimilarity	factorial PERMDISP (*BC*)	$F = 52.3_{3,48}$ $p < 0.001$	$F = 21.6_{2,48}$ $p < 0.001$	$F = 1.2_{6,48}$ $p = 0.33$
Compositional Dissimilarity	factorial PERMDISP (*J*)	$F = 51.7_{3,48}$ $p < 0.001$	$F = 20.1_{2,48}$ $p < 0.001$	$F = 2.7_{6,48}$ $p < 0.025$
Compositional Dissimilarity	one-way PERMDISP (*BC*)	N/A (Low propagule only)	$F = 11.3_{3,16}$ $p = 0.004$	N/A
Compositional Dissimilarity	one-way PERMDISP (*BC*)	N/A (Mid propagule only)	$F = 5.1_{3,16}$ $p = 0.009$	N/A
Compositional Dissimilarity	one-way PERMDISP (*BC*)	N/A (High propagule only)	$F = 1.2_{3,16}$ $p = 0.35$	N/A

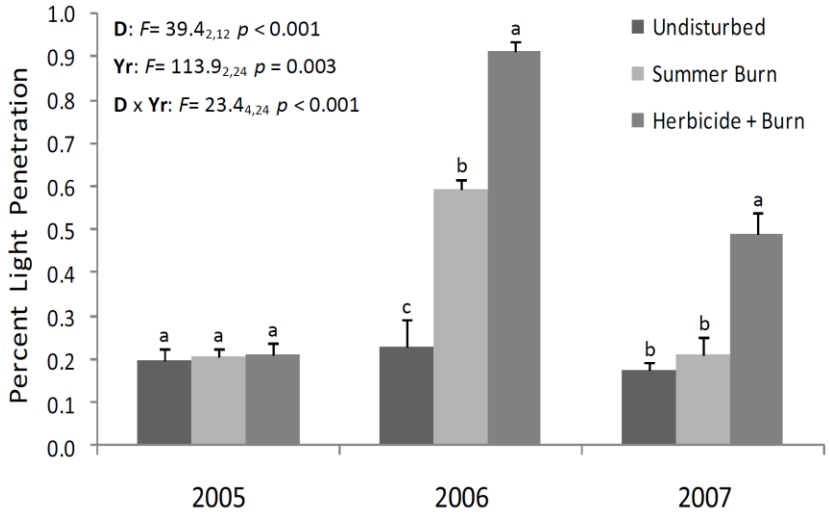

Figure 1 Mean percent light penetration (+1 SE) for each disturbance treatment for 2005 through 2007 illustrates variation in light availability in response to disturbance. Significant effects of Disturbance (D), Year (Y), and Disturbance x Year (DxY) interactions are indicated by repeated measures ANOVA. Significant differences ($p < 0.05$) among disturbance treatments within years are denoted by the absence of a common letter.

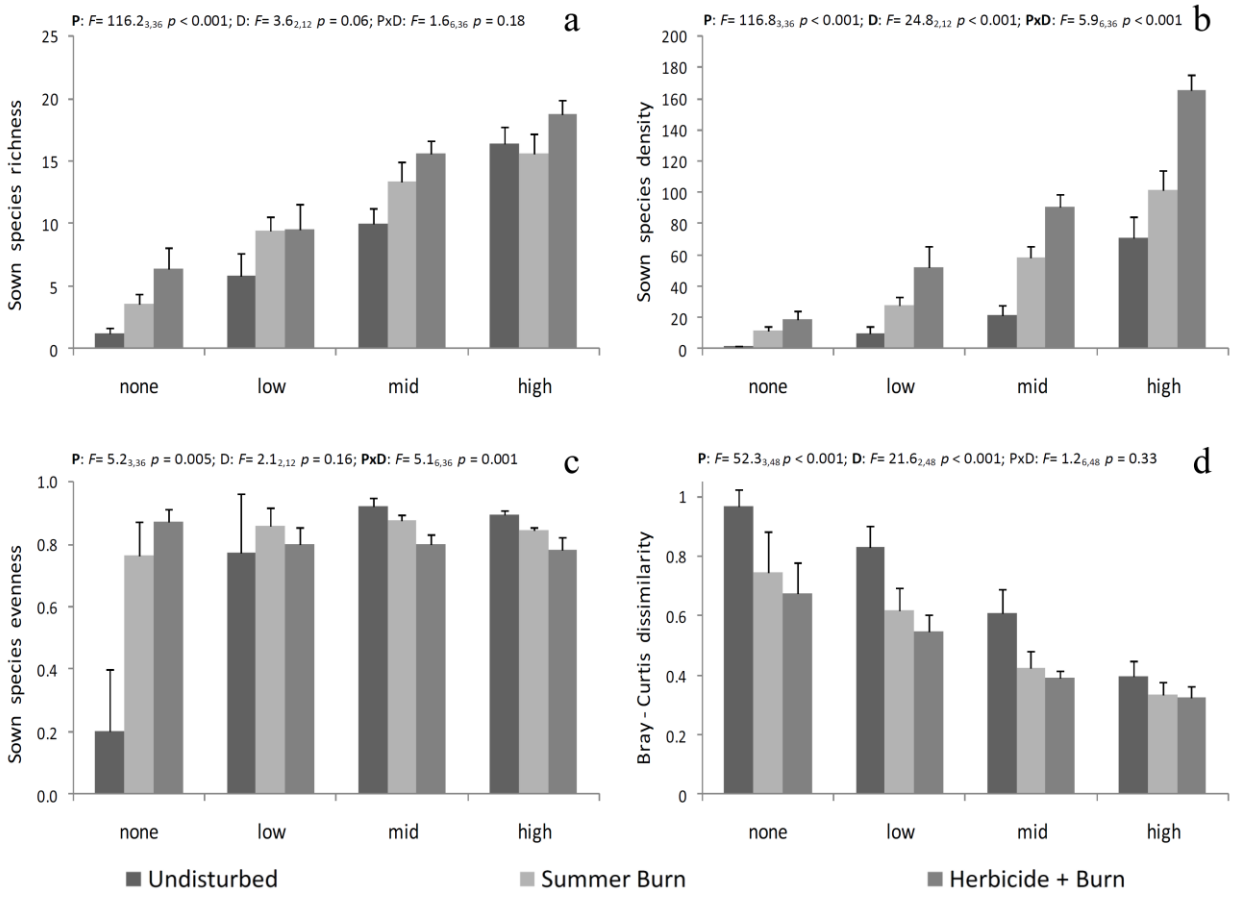

Figure 2 Mean richness (a), density (b), evenness (c), and Bray-Curtis dissimilarity (d) of sown species for disturbance treatments across each level of propagule pressure. Mean Bray-Curtis dissimilarity (d) is the average of all pairwise comparisons of dissimilarity for quadrats within each factorial treatment group. Dissimilarity ranges from 0 when the composition and relative abundance of species between two quadrats is identical to 1 when no species are shared. Error bars represent + 1 SE for figures a-c and a 95% confidence interval for figure d. Results from repeated measures ANOVA (a-c) and PERMDISP (d) indicate effects of Propagule Pressure (P), Disturbance (D), Propagule x Disturbance interactions (PxD) on response variables.

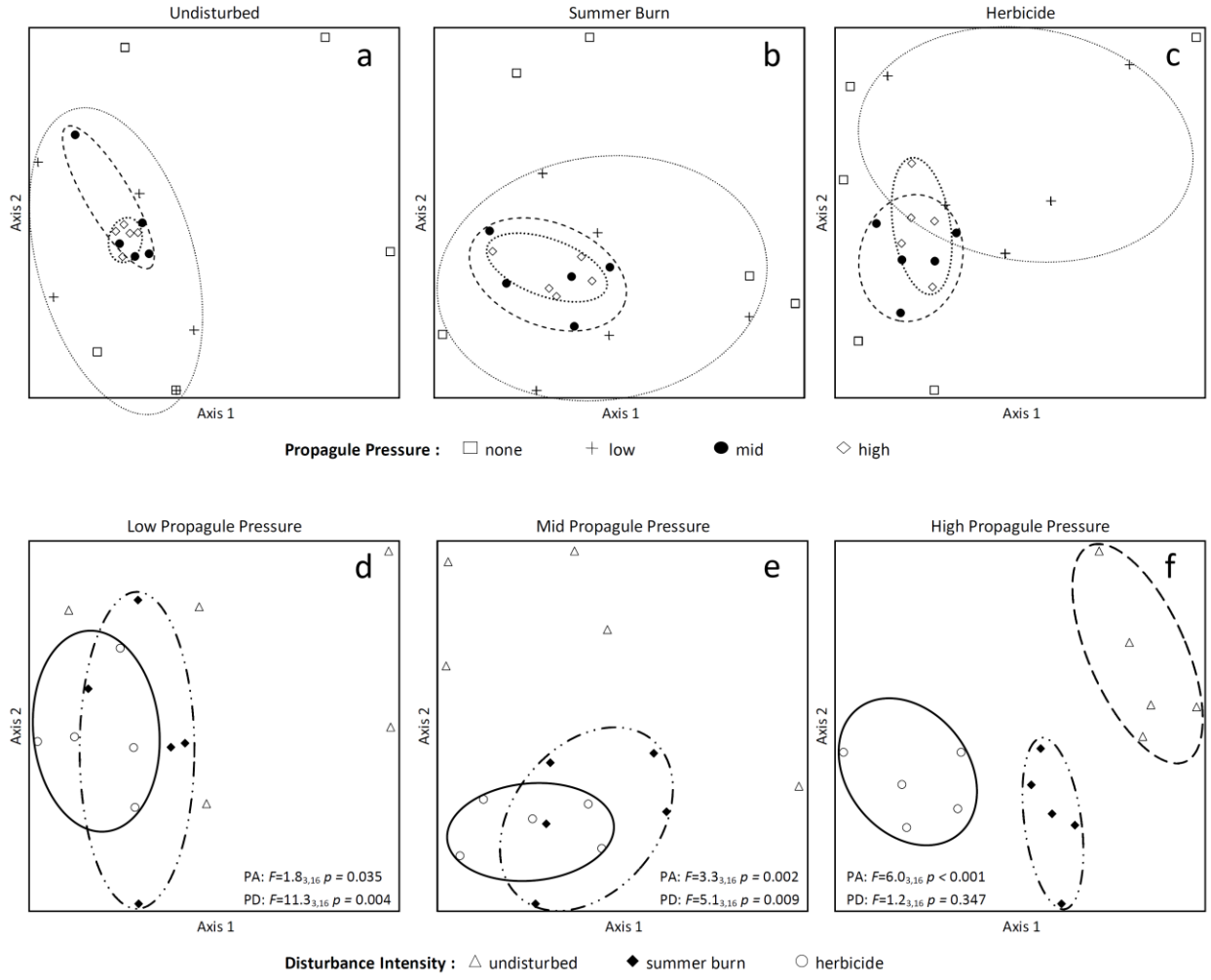

Figure 3 Non-metric multidimensional scaling (NMDS) illustrates the community composition of sown species in sampling quadrats for all levels of propagule pressure within each disturbance treatment (a-c) and for each disturbance treatment at low (d), mid (e), and high (f) propagule pressures. NMDS ordination of unsown plots couldn't be completed due to weakly structured data. The Euclidean distance between points illustrates the difference in Bray-Curtis dissimilarity between communities. Results of one-way PERMANOVA (PA) and PERMDISP (PD) indicate significant differences in community composition and within-in group dispersion, respectively, between disturbance treatment groups within levels of propagule pressure.

Chapter 2

Trait-based recruitment in grasslands:

a synthesis of tallgrass prairie restoration studies

CHAPTER SUMMARY

To examine the role of plant traits in regulating species recruitment in grassland restorations, we compiled and analyzed data on initial establishment from 54 seed addition studies conducted throughout the tallgrass prairie region. We quantified 10 traits for each of the 190 native prairie species sown in the compiled studies. Analyses demonstrated increased recruitment potential associated with flowering during mid to late summer, long flowering duration, intermediate height, and clonality. Additionally, species with intermediate seed mass had the greatest recruitment potential despite expectations that large-seeded species would exhibit consistently high recruitment when dispersal limitations were eliminated through seed addition. Although a favorable trait does not assure successful recruitment, advantageous traits set a higher upper bound on recruitment potential than disadvantageous traits. Recruitment potential is greatest when beneficial values for traits such as seed mass and height act in concert, but recruitment can be severely limited by syndromes of disadvantageous traits. While the predictive power of these findings is limited, this study has illuminated general trait-based recruitment patterns that emerge across varied environmental contexts of the tallgrass prairie region and established a foundation for future research that is needed to integrate trait-based knowledge into management practice. A greater understanding of how plant traits influence recruitment holds the potential to further our understanding of community assembly and facilitate ecosystem restoration and management.

INTRODUCTION

Interpretation of ecological patterns and processes via the traits expressed by species has emerged as an important means of addressing fundamental questions in ecology. The recent expansion of trait-based approaches has generated novel perspectives across ecological sub-disciplines, addressing a diverse array of subjects from microbial biogeography (Green *et al*. 2008) and phytoplankton community structure (Litchman *et al*. 2007) to global soil carbon sequestration (De Deyn *et al*. 2008) and ecosystem response to climate change (Suding *et al*. 2008). In the field of plant ecology, traits have been used to examine subjects such as community assembly (Fukami *et al.* 2005, Ackerly and Cornwell 2007), meta-population dynamics (Dupre and Ehrlen 2002), habitat fragmentation (Kolb and Diekmann 2005), and invasion (Thompson *et al.* 2001). Given that environmental filters act upon traits rather than species (Keddy and Weiher 1999), there is mounting support for addressing ecological questions using trait-based classifications rather than taxonomic units to increase the generality of findings and promote common rules for community ecology (Cornelissen *et al*. 2003, McGill *et al*. 2006). To aid the growth of this developing field, expansive trait databases are being developed including the LEDA traitbase for Northwestern European Flora (Kleyer *et al*. 2008) and the Global Plant Trait Network (Wright *et al.* 2004). The advancement of traits as a universal measure for comparisons across species, communities, and environmental gradients has great potential to broaden our understanding of fundamental issues in basic and applied ecology.

Understanding the role of plant traits in determining patterns of diversity is a basic ecological objective with applications to conservation and restoration practice. A thorough understanding of coexistence in plant communities is essential for the advancement of management practices that increase species richness, conserve biodiversity, and inhibit invasion by exotics. Traits are

fundamental to the interpretation of classical models of coexistence such as limiting similarity and niche partitioning. Limiting similarity inherently relies upon trait divergence among proximate species to avoid competitive exclusion and permit localized coexistence (Pacala and Tilman 1994, Weiher *et al*. 1998). In addition, recent works promote trait-based quantification of fundamental niches across environmental gradients and emphasize the potential of functional traits to predict competitive outcomes that determine realized niches (McGill *et al*. 2006, Violle and Jiang 2009). Spatial coexistence in local communities may also be explained by competition-colonization tradeoffs, in which competitively superior species cannot achieve uniform dominance due to dispersal limitations (Tilman 1994). It is suggested that allocation constraints associated with traits such as seed mass (Levine and Rees 2002, Turnbull *et al*. 2005) and clonality (Eriksson 1989) result in tradeoffs between dispersal and competitive ability. If species abundances in natural communities are maintained by dispersal limitations (Erikkson and Jakobsson 1998), recruitment should dramatically increase when dispersal limitations of superior competitors are negated by seed addition. Accordingly, analysis of seed addition and restoration studies permits examination of recruitment patterns in isolation from the effects of dispersal.

Although restoration ecology is a rapidly developing field, prairie restorations rarely approach the diversity of remnant prairies (Kindscher and Tieszen 1998, Martin *et al*. 2005). For restorations to achieve greater diversity, the science of restoration must address mechanisms responsible for plant coexistence and response to restoration practice (Young *et al*. 2005). Given that recruitment is an essential precedent for species coexistence, a comprehensive understanding of interactions between plant traits and recruitment could guide efforts to more closely approximate the diversity of remnant reference communities. Despite substantial potential, trait-based analyses have seldom been explored in restoration ecology. While previous studies have

utilized traits to suggest guidelines for increasing invasion resistance of restored plant communities (Funk *et al*. 2008), to identify target species for oak savanna restoration from a regional species pool (Brudvig and Mabry 2008), and to examine species performance in restored calcareous grasslands (Pywell *et al*. 2003), the relationship between plant traits and species recruitment in tallgrass prairie restorations has not been previously investigated.

This study examines relationships between plant traits and the restoration of tallgrass prairie species by analyzing data on initial recruitment from 54 seed addition studies. Due to the scarcity of long-term datasets, this study examines initial recruitment rather than persistence and fecundity of sown species. While assessing trait relationships with long-term persistence may provide additional insight, early life stages of germination and initial recruitment are the most restrictive determinants of plant community structure and diversity (Weiher and Keddy 1995, Kitajima and Tilman 1996). Given that individual studies can be shaped by localized environmental conditions and stochastic events, examining the generality of ecological patterns requires data synthesis from numerous studies encompassing a large geographic scale (McIntyre *et al*. 1999, Goldberg *et al*. 1999). Certainly factors such as climate, soils, geography, and disturbance substantially impact recruitment, but our purpose here is to identify common trait-based recruitment patterns that emerge in spite of such environmental variation. While the predictive power of our findings is constrained by the inclusive nature of this approach, analyses of numerous species from experiments throughout the tallgrass region illustrates persistent relationships between plant traits and recruitment in grassland restorations.

Traits and hypotheses

In order to obtain trait values for the multitude of species for which we compiled recruitment data, the traits examined in this study (Table 1) were primarily "soft" traits that can be readily quantified and serve as analogs for more difficult measures of ecological function (Weiher et al. 1999, Lavorel and Garnier 2002, Cornelissen 2003). While a comprehensive trait database for the North American flora is planned (http://www.columbia.edu/cu/traitnet), data for traits such as specific leaf area and leaf water content that might ideally be analyzed in relation to initial recruitment is not presently available for the vast majority of species in the tallgrass prairie region. Given that field measurement of functional traits for a large number of species can be logistically impractical, examination of relevant soft traits allows replication of methodologies and facilitates comparisons across regions and community types (McIntyre et al. 1999, Weiher et al. 1999, Westoby et al. 2002).

We expected traits associated with establishment and competitive ability, rather than natural dispersal, to be indicators of successful recruitment given that seed was intentionally sown in the compiled datasets. We hypothesized that increased recruitment potential would be associated with large seed mass, increased height, late-season flowering, and clonal growth. Seed size variation in natural plant communities is associated with a tradeoff between competitive and dispersal abilities (Westoby *et al.* 1990, Turnbull *et al.* 1999, Levine and Rees 2002). Small-seeded species generally produce more seeds per individual, disperse farther distances, and have superior seed bank longevity (Harper *et al*. 1970, Guo *et al*. 2000). Conversely, carbohydrate reserves in the endosperm of large seeds enhance recruitment during stressful environmental conditions (Rees *et al.* 1993), and large seeds generally produce larger seedlings (Leishman *et al.* 2000) that are often able to out-compete smaller seedlings during the critical stages of initial

recruitment. Because experimental seed additions can negate dispersal limitations of large-seeded species (Turnbull *et al*. 2005), we expected that increased seed mass would demonstrate a distinctly positive effect on recruitment in our dataset.

In addition to seed mass, height has been identified as a reliable predictor of competitive ability (Weiher *et al*. 1999). Acceptance of this relationship is so pervasive that some field experiments use height as a surrogate measure of competitive ability (Gaudet and Keddy 1995, Bullock *et al*. 2001). The advantage of increased height results from greater access to light and the concurrent shading of neighboring plants. Comparative studies of plant height have primarily focused on forested communities in which the remarkable heights attained by trees result in considerable tradeoffs between allocation to structural versus photosynthetic tissues (Westoby *et al*. 2002). However, even in the high light environment of tallgrass prairie the ability to attain greater height than neighboring plants may confer a considerable advantage through competition for light, especially in highly productive plant communities (Foster 2001). Accordingly, we hypothesized that increased height would enhance recruitment in grassland restorations.

Although flowering time is an adult trait not directly linked to juvenile growth, flowering time is indicative of seasonality (Weiher *et al.* 1999) among tallgrass prairie species and is commonly defined in regional floras, whereas explicit data on active growth period is less widely available. Logically, early-flowering species have an active growth period that precedes late-flowering species and vice versa. Droughty conditions often encountered in the tallgrass region during mid to late summer should select for increased drought tolerance among species with active growth and flowering during these times, leading us to hypothesize that recruitment would be enhanced among late-flowering species.

Increased ability to exploit localized resource patches through clonal growth is a measure of competitive vigor (Cornelissen *et al*. 2003) that is thought to compensate for scarcity of seedling recruitment among clonal plant populations, and represents a competition-colonization tradeoff between allocation to vegetative and sexual reproduction (Olejniczak 2001). The relaxation of dispersal limitations through seed addition has been shown to increase recruitment among clonal species in restored calcareous grasslands (Pywell *et al*. 2003), and we hypothesize that clonality will also enhance recruitment among tallgrass prairie species.

Although the aforementioned traits of seed mass, height, flowering time, and clonality are predicted to be the strongest determinants of initial recruitment among the traits examined, other traits thought to be pertinent for recruitment and persistence in plant communities warrant further consideration. Grasses, particularly warm-season C_4 species, are widely believed to exhibit superior recruitment to forbs in tallgrass prairie restorations and may ultimately inhibit the successful colonization of native forbs (Weber 1999), leading us to examine photosynthetic pathway and recruitment differences among forbs and grasses. The increased efficiency of the C_4 photosynthetic pathway under severe heat and drought stress could be very beneficial for recruitment and survival in the tallgrass region. Annual and biennial species were also expected to exhibit high recruitment rates given the affinity of these species for disturbed and open habitats (McIntyre et al. 1999) that are often associated with restorations. Variation in leaf area gives rise to a tradeoff in which the greater surface area of large leaves enhances photosynthetic capacity and relative growth rate, while small leaves exhibit greater tolerance of drought and extreme temperatures (Weiher *et al*. 1999, Westoby *et al*. 2002, Cornelissen *et al*. 2003). Consequently, the potential advantage of divergent leaf size strategies for recruitment in the tallgrass region may preclude the emergence of a consistently superior strategy. Capacity for

nitrogen fixation is often associated with increased growth rate (Lavorel and Garnier 2002), though the contingency of this beneficial response upon localized nutrient limitations (Cornelissen *et al*. 2003) may limit the reliability of this trait as a generalized predictor of recruitment across restorations. Flower duration was examined because prolonged flowering period has been identified as a unifying trait among species that successfully colonize following fire and soil disturbances (Lake and Leishmann 2004, Moretti and Legg 2009) which are commonly prescribed during restoration, though the connection between this adult trait and seedling recruitment is poorly understood.

Although we hypothesize that certain individual traits will influence recruitment, species possesses suites of traits that may collectively affect recruitment potential. It is predicted that non-additive interactions among beneficial traits will further increase recruitment potential. Furthermore, traits that are not independently significant may affect recruitment through interactions when expressed concurrently with other traits. While there is no singular strategy for successful recruitment, this study identifies key traits and trait interactions indicative of recruitment potential across the broad geographic range of the tallgrass prairie.

METHODS

To identify prospective studies, we conducted an extensive literature survey using the ISI Web of Knowledge electronic database to search for articles from all available years using the following Boolean search: (prairie* or grassland*) and (colonization or establishment or recruitment) and (seed addition* or restoration*). We also obtained and surveyed hard copies for every issue of

the journals *Ecological Restoration* and *Proceedings of the North American Prairie Conference*, which were unavailable electronically. Numerous individuals and organizations active in the field of tallgrass prairie restoration were personally contacted and generously shared data. We screened potential studies to include only experiments with practical methodologies for large scale restorations, documented seeding rates for each species sown, and subsequent records of stem counts, percent cover, and/or plot occupancy data to quantify initial recruitment. In total, we compiled 54 seed addition datasets from 8 states (Table 2) that included 190 native prairie species (Table 3). Multiple datasets from the same author or organization were included if they were conducted in different years or geographic locations, or used different seed mixes and restoration practices. The duration between seed addition and data collection ranged from 1 to 4 growing seasons among the compiled studies, with the majority of data recorded in the second growing season at an average of 17 months post-seeding. Preliminary regression analyses revealed no effect of study duration on recruitment, and data were not filtered on this criterion.

Recruitment metrics

The term *recruitment* is used throughout this paper as a general reference to the process in which individuals are incorporated into the local plant community, but for the purposes of this study does not encompass dispersal aspects of recruitment because seeds in the compiled studies were intentionally sown. In adherence with the recommendations of Englund *et al*. (1999) that multiple criteria be used to explore statistical conclusions, we conducted analyses using three quantitative metrics: *percent establishment*, *frequency*, and *presence*. Percent establishment is defined as the percentage of sown seed that established, and was calculated as stems/m^2 divided by the approximate number of seeds sown per square meter for each species in a given study.

Frequency is defined using plot occupancy data to calculate the proportion of plots in each study in which a given species was observed. Presence is defined as 1 or 0 for each study in which a species was sown based on whether the species was present or absent. Percent cover was dropped as a potential metric after exploratory analyses because it is more indicative of plant size than successful recruitment per se. The intrinsically small stature of a species should not be interpreted as poor recruitment. However, percent cover was used in conjunction with stem counts and plot occupancy data to qualify that a species was present in a study.

Treating each occurrence of a trait associated with a particular species sown in multiple studies as an independent value in analyses of the relationships between traits and recruitment would be pseudoreplication, so we calculated a mean value per species for each recruitment metric prior to analyses. We also weighted mean recruitment metric values per species by the number of studies in which each species was sown. Given that not all studies measured stem counts, plot occupancy, and cover values, the three metrics could not be quantified for every species in the synthetic dataset. Percent establishment was calculated for 89 species, frequency for 162 species, and presence for 190 species. The resulting data matrix was comprised of 190 rows, 1 per species, with columns for mean recruitment metric values and corresponding trait measures for each species.

Trait values

We obtained values for growth form, longevity, clonality, plant height, leaf area, flowering time, and flowering duration from The Flora of the Great Plains (McGregor *et al.* 1986) or Manual of the Vascular Plants of Northeastern United States and Adjacent Canada (Gleason and Cronquist 1991) if values for a species were absent in the former. Following the protocol of Farnsworth

(2007), we calculated plant height as the mean of maximum and minimum published values, leaf area as the area of an ellipse formed by the average of maximum and minimum values for leaf length and width, flowering time as the median reported flowering month, and flowering duration as the maximum number of days a species is in flower based on the flowering period reported in regional floras. We classified growth form as graminoid or forb and longevity as annual, biennial, or perennial. Exploratory analysis confirmed the assertion of Weiher *et al*. (1999) that there is little benefit to further designation of perennials into Raunkiaer life forms for trait-based analysis. We treated clonality as a simple binary trait, given the problematic nature of quantifying extent of clonal growth (Cornelissen *et al*. 2003). We assigned values for C_3 versus C_4 photosynthetic pathway and nitrogen fixation capacity by referring to Freeman (2002). To resolve any uncertainties regarding trait classifications we consulted with staff of the R.L. McGregor Herbarium at the University of Kansas. We acquired seed mass data from the Kew Seed Information Database (Liu *et al*. 2008) and from the Prairie Moon Nursery catalog (http://www.prairiemoon.com) for the small subset of species not quantified by the former. Seed mass values were Log_{10} transformed prior to analyses. We acquired current species nomenclature from the USDA PLANTS database (USDA-NRCS 2009).

Statistical analysis

Statistical procedures for meta-analysis generally utilize within-study sample error to calculate standardized effect size metrics for the comparison of multiple treatments. Though this study is meta-analytical in nature, our analysis is not amenable to a standard meta-analytical approach because we are not explicitly comparing two or more treatment conditions and the reporting of within-study sample error varied among the compiled studies. When data limitations preclude

the calculation of standardized effect size metrics, relevant insights can be gained through analysis without strict meta-analytical procedures (Gurevitch and Hedges 1999). Accordingly, we opted not to exclude data or otherwise narrow the scope of our inquiry by conforming to statistical procedures which poorly suit the objectives of this study.

To verify the significance of recruitment variation among species in the compiled dataset (Fig. 1), we conducted Kruskal-Wallis one way analysis of variance tests using raw recruitment metric values per species across all studies. Mean recruitment metric values per species were used as response variables in all subsequent analyses that examined traits, rather than species identities, as predictors of recruitment.

We used generalized linear models to determine which plant traits influence percent establishment and frequency in the compiled restoration dataset. We used logistic regression models for presence data because the recruitment response was binary; each species was either present (yielding a value of 1) or absent (yielding a value of 0) in each study. Mean values for recruitment metrics were weighted in the analyses by the number of studies in which each species was sown. The ten traits were entered into models using a backward elimination process to determine main effect predictors of recruitment for all metrics. We then examined models with two-way interactions between traits to determine the influence of multiplicative trait combinations on recruitment. Although there were inter-correlations among traits, measures of collinearity for each model were determined to be within acceptable limits (Norisus 2009). To consider potential effects of phylogenetic relationships we repeated regression models using mean trait values for genera and families as predictors of recruitment.

Given that the recruitment response distribution of seed mass (Fig. 2) and height (Fig. 3) were non-linear envelope relationships insufficiently portrayed by regression models, we

performed Chi-square tests to determine whether the observed patterns differed from expected random distributions. We binned percent establishment and frequency values into quintiles of log-transformed seed mass with roughly equal numbers of observations, thus partitioning the distributions of percent establishment and frequency in relation to seed mass into 5 x 5 grids. We then compared the observed distribution to a uniform distribution on [0,1] x [0,1], which assumes that points are evenly distributed across all potential seed mass and recruitment metric combinations. This procedure was repeated for the distribution of height in relation to percent establishment and frequency. Kolmogorov-Smirnov tests were used to examine distributions of percent establishment and frequency among classes of flowering duration and flowering time. Statistical analyses were performed using the R statistical package version 2.9.0 (The R Foundation for Statistical Computing 2009).

RESULTS

Kruskal-Wallis tests confirm that recruitment differs significantly among species in terms of percent establishment (H=517.9; d.f.=88; P<0.0001), frequency (H=433.2; d.f.=161; P<0.0001), and presence (H=668.1; d.f.=189; P<0.0001). The distribution of mean species frequencies (Fig. 1) exemplifies the tremendous variation in recruitment among species sown in prairie restoration experiments. While trait relationships are consistent among recruitment metrics, the distribution of recruitment success among sown species (Fig 1.), like the figures for seed mass (Fig. 2) and height (Fig. 3), is illustrated using mean frequency because this metric is quantified for a greater

number of species than percent establishment and provides finer visual resolution than mean presence, which is based upon a binary response.

The traits retained as significant predictors of recruitment probability in the backward elimination logistic regression model of mean species presence (null-residual deviance =181, d.f.=11, AIC =930.7) were seed mass, flowering duration, flowering time, height, and clonality (Table 4). The model demonstrates highly significant positive effects of clonality ($P<0.0001$), seed mass ($P<0.0001$), and height ($P<0.05$) on recruitment probability, though the parameter estimates for height and seed mass are logically limited given the more unimodal distribution of recruitment in relation to these traits. The probability of species presence is significantly higher among species in flowering duration classes of 90 days or greater ($P<0.05$), and summer flowering species demonstrate significantly greater recruitment probability ($P<0.0001$) relative to species flowering in May. Graphical representation of presence also illustrates that species with unfavorable values for these significant traits are less frequently sown in restorations (Fig. 5). Despite the high significance of traits retained as main effects in the logistic regression model, the parameter estimates of these traits and the overall model fit were poor (Table 4). Generalized linear models for percent establishment and frequency exhibited even less predictive power, but retained the same significant main effects as the logistic regression model for presence.

Inclusion of trait interaction terms improved AIC values of logistic regression models for mean presence. Traits that were not retained in the main effects model were likewise insignificant ($P>0.05$) when incorporated into interactions. Although most trait combinations do not influence recruitment in more than an additive fashion, certain significant interactions are repeatedly retained by model variants. We evaluated interaction models based upon model

significance and AIC values to arrive at three model variants (Table 5), among which no single model was substantially superior. Although there is no singular ideal model, the models collectively demonstrate significant positive interactions between flowering duration and flowering time, flowering duration and seed mass, flowering time and seed mass, flowering time and height, and seed mass and height. In each of the model variants the positive interactions demonstrating enhanced recruitment among species with mid-to-late summer flowering time and long flowering durations have parameter estimates with at least twice the value of other significant interactions, indicating the value of these trait combinations as indicators of recruitment success. The lack of significant interactions between the longest flowering duration classes and late season flowering times results because there are no species in the dataset that express these hypothetically beneficial but ecologically improbable trait combinations. The significant trait combinations that emerge when interactions are included in logistic regression models emphasize that multiple traits act in concert to affect recruitment potential.

When regression models were conducted using mean trait values per genus, traits retained as significant predictors of recruitment did not differ from models based on individual species. Models using mean values per family yielded no traits to be significant predictors of recruitment. The compiled dataset includes 190 species from 123 genera and 33 families. The vast majority of genera are only represented by one species and significant trait relationships are not biased by potential non-independence among congeners. Conversely, trait values and recruitment rates within families are far too variable for significant patterns to emerge at that scale.

Chi-square tests demonstrate that fine scale recruitment patterns measured by percent establishment and frequency are highly constrained by seed mass and plant height. The observed distributions of frequency as a function of seed mass (χ^2 =83.2; d.f.=16) and height (χ^2 = 147.2;

d.f.=16) and percent establishment as a function of seed mass (χ^2 =477.6; d.f.=16) and height (χ^2 =595.5; d.f.=16) are all significantly different (P<0.0001) from uniform distributions on the interval [0,1] x [0,1]. Although the reported test statistics result from partitioning each distribution into quintiles, the high significance of χ^2 values was insensitive to how the observed distributions were partitioned. It is evident that species with intermediate seed mass have the highest upper bound on recruitment potential, although there is substantial recruitment variation among these species that may be partially explained by interactions with other traits (Fig. 2). Recruitment potential is greatest among species with moderately tall height, though performance declines among exceptionally tall species in the dataset (Fig. 3).

Kolmogorov-Smirnov tests indicate that distributions of percent establishment and frequency are not constant across categories of flowering duration or flowering time (Fig. 4). Frequency distributions differ significantly among trait classes, and species with a 120 day flowering duration exhibit higher frequency than those with a 60 day flowering duration (D=0.371, P<0.05). Relative to species flowering in May, July flowering species exhibit higher frequency (D=0.515, P<0.001) and percent establishment (D=0.608, P<0.05), and September flowering species exhibit higher frequency (D=0.509, P<0.01). Cumulative distribution functions (Fig. 4) further illustrate that species flowering in May and species with short flowering duration have constrained recruitment potential relative to other classes for these traits.

Collectively, the analyses argue that seed mass, height, flowering duration, flowering time, and clonality are important determinants of initial recruitment potential. Significant trait interactions illustrate that recruitment is influenced by unique combination of traits acting in concert. Seed mass and height place significant constraints on recruitment, with intermediate values of each providing the greatest potential for success. Overall, models used to infer the

influence of traits on recruitment have limited predictive power despite high significance. While limited predictive power may reflect the importance of environmental factors not accounted for by trait-based analysis, these models do illuminate suites of traits linked to species performance. The substantial unexplained variability illustrates that particular traits or trait combinations do not guarantee universal recruitment success, but conversely, it is possible with considerable certainty to outline trait combinations such as short height and early flowering time that confer an imposing probability of failure.

DISCUSSION

The restoration of diverse plant communities represents "the greatest challenge and opportunity for restoration ecology" (Young *et al.* 2001). The failure of most prairie restorations to capture the diversity of intact remnant prairies must be addressed to improve the aesthetic, conservation, and ecosystem value of these communities. A greater understanding of the relationship between plant traits, resource requirements, and disturbance responses may facilitate the realization of these restoration objectives (Funk *et al*. 2008). In our analyses we have identified key traits associated with the recruitment of native prairie species and the diversity of restored grasslands. Out of necessity many of the traits analyzed in this study were "soft traits" employed as surrogates for more difficult to quantify "hard" traits, which in turn estimate true function (Weiher *et al.* 1999). This distance between traits that were analyzed and true ecological function may contribute to poor model fits. Although the predictive power of these findings is limited, it is of substantial interest that these traits demonstrate significant effects on recruitment across

broad geographic ranges despite the plasticity which plants exhibit and the considerable variation in location, climate, and management regimes among the many datasets included in the analyses.

It is interesting to note that there is a positive relationship between the number of studies in which a species was sown and its recruitment probability, with no species sown in 20 or more studies failing to establish (Fig. 5). However, the relatively high recruitment among commonly sown species is not responsible for the trait relationships observed in this study. There is no systematic association between a particular trait, the number of times that a species expressing that trait was sown, and its probability of success (Fig. 5; Fig. 2a). Furthermore, recruitment metrics were weighted by the number of studies in which species were sown, and exclusion of the most frequent and/or infrequently sown species from analyses does not alter significant trait-based recruitment patterns. The successful recruitment of frequently sown species is a logical result of researchers preferentially selecting species that are commonly perceived to perform well in restorations. There is a general knowledge of which species reliably establish in restorations even if the underlying effects of plant traits have been poorly defined.

Traits and interactions that are significant in the statistical models are tangibly exemplified through consideration of the character combinations possessed by species with the highest recruitment. *Helianthus maximiliani* (Maximilian sunflower) and *Salvia azurea* (blue sage) rank 1st and 2nd respectively among all species in terms of percent establishment and frequency, and both species were present in all studies in which they were sown. *H. maximiliani* is a strongly clonal species with an average height of 150cm that flowers from August to October, while *S. azurea* has solitary or multiple stems with an average height of 100cm and flowers from July to October. Both of these species are relatively tall with long flower durations in the mid to late growing season and intermediate seed masses.

Although it is apparent that disadvantageous traits such as low seed mass can severely restrict recruitment potential, it is incorrect to presume that beneficial traits will consistently confer high recruitment rates. There is considerable variation among species with intermediate seed mass and some exhibit very low recruitment (Fig. 2). It is more judicious to state that beneficial traits such as intermediate seed mass set a high upper bound on recruitment potential. Recruitment is affected by interactions among multiple traits, some of which vary independently, and recruitment potential may be constrained by the lowest common denominator among the suite of traits expressed by a given species. This concept is illustrated by the variation in recruitment among three composite species with intermediate seed masses. The aforementioned *Helianthus maximiliani*, with a 2.0mg seed mass, 150cm height, and strongly clonal growth exhibits a frequency of 84.2%. *Coreopsis palmata* also has a 2.0mg seed mass and is clonal, but has a lesser height (65cm) and exhibits moderate recruitment with a frequency of 31.2%. Lastly, *Echinacea angustifolia* has a 2.6mg seed mass, but is not clonal, has a short height (35cm), and exhibits very low recruitment frequency of 1.5%. Consequently, unfavorable traits like short height may constrain species recruitment potential despite expression of other beneficial traits.

Seed mass

Among the 190 species we examined, there is a 260-fold difference in seed mass between the miniscule 0.3mg seeds of *Triodanis perfoliata* and the 78mg seeds of *Silphium laciniatum*. Although we confirmed a significant positive effect of seed mass on recruitment across this spectrum, this relationship is not linear and indicates superior recruitment potential among species with intermediate seed masses (Fig. 2). As predicted by competition-colonization tradeoff hypotheses associated with seed size variation, species with intermediate sized seeds

have been found to exhibit the highest natural abundance in grassland communities (Eriksson and Jakobsson 1998). However, this result was not anticipated in our dataset given the relaxation of dispersal limitations, and our analyses illustrate that post-dispersal tradeoffs can also favor recruitment of species with intermediate seed mass in grassland restorations.

The moderation of recruitment among species with very large seed mass may result from these species being disproportionately affected by seed predation (Venable and Brown 1988, Guo *et al*. 2000). Seed predation by rodents, birds, and invertebrates can significantly affect the structure and composition of grassland communities (Hulme 1994, Reed *et al*. 2004). Although the generality of a relationship between predation and seed size across ecological communities is disputed (Moles and Westoby 2004), studies of seed predation in tallgrass prairie restoration experiments indicate that vertebrate predation reduces the density of competitively superior large-seeded species and can alter the assembly of early successional communities (Howe and Brown 2001). Disproportionate post-dispersal predation of large-seeded species could enact a competition-predator avoidance tradeoff that favors recruitment of intermediate sized seeds. Species that may have been limited by predation include *Silphium laciniatum* (compass plant) *and S. integrifolium* (rosinweed), which have fleshy seeds with soft seed coats and exhibited limited recruitment despite being among the 5 highest seed mass values in our dataset. Given that seed sowing density is positively related to seed encounter and predation, decreasing propagule density could potentially lower predation rates for large-seeded species (Hulme 1994).

While increased predation on large-seeded species is a plausible explanation for the unimodal relationship between seed mass and recruitment observed in this study, other physiological and environmental factors may contribute to this pattern. Large-seeded species with dense seed coats can have significantly increased germination in response to scarification (Boyle and Hladun

2005). Delayed germination in the absence of scarification could prolong exposure to seed predation. Additionally, priority effects could result in the exclusion of competitively superior species with delayed germination if other species more rapidly exploit available resources. Species with dense seed coats such as *Psoralidium tenuiflorum* and *Tephrosia virginiana* had only moderate recruitment success despite having among the largest seeds in this study, possibly due to lack of scarification prior to sowing in many experiments.

Plant height

Despite the expectation of a positive linear relationship between height and recruitment, species with intermediate height exhibit the highest upper bound on recruitment potential while species at either extreme of the height spectrum generally exhibit low recruitment (Fig. 3). Increased height may be beneficial until a threshold of allocation towards shoot growth is exceeded, incurring a costly tradeoff that yields root structures inadequate to support disproportionately large aerial biomass during droughty conditions. This possible tradeoff appears to be less pronounced among clonal species, as exceptionally tall species with extremely low recruitment values were all non-clonal. In addition, while regression model interactions between increased height and seed mass indicate an overall positive recruitment response, exceptionally tall, large-seeded species had poor recruitment that may be attributed to the aforementioned disadvantages associated with very large seed mass.

Although extreme height may be disadvantageous for many species, regression model interactions demonstrate that taller species flowering late in the growing season exhibit high recruitment potential, and a significant positive correlation was observed between plant height and flowering time ($r = 0.487$, $P < 0.001$). Increased height may be markedly advantageous for

late-season species because light availability is enhanced by obtaining greater stature than species with peak growth earlier in the season.

Flowering time

Species with peak flowering time in mid to late summer exhibited markedly higher recruitment potential than May flowering species (Fig. 5a-b). This pattern may result from selection for drought tolerance among species with active growth periods during the mid-late summer, in addition to the aforementioned positive correlation between height and flowering period. Among the late-flowering species with high recruitment are the dominant and drought tolerant C_4 grasses *Sorghastrum nutans* (Indiangrass), *Andropogon gerardii* (big bluestem), and *Panicum virgatum* (switchgrass), which have been found to inhibit the recruitment of less competitive forb species when sown concurrently in restorations (Dickson and Busby 2009). Mid to late season forbs with high recruitment in the analyses include species such as *Salvia azurea*, *Ratibida pinnata*, *Chamaecrista fasciculata*, *Symphyotrichum novae-angliae*, *Solidago spp*., and *Helianthus spp*., all of which are recognized for their dependable performance in tallgrass restorations and are often included in Conservation Reserve Program seed mixes.

Flowering phenology also influences vegetative response to the timing of disturbances in tallgrass prairies, particularly the seasonality of prescribed burns. Prescribed dormant season burns can darken and expose the soil surface, thereby raising surface temperatures to induce earlier onset of growth and increased productivity among dominant warm season grasses, resulting in the inhibition of early-flowering forb species (Howe 1994). Accordingly, prescribed burns commonly employed as seed bed preparation or ongoing management during the initial years of restorations could contribute to poor recruitment of early-flowering species. Restoration

practitioners should consider management regimes which vary the seasonality of prescribed burns, mowing, grazing and other disturbances to facilitate recruitment of early-flowering species by tempering the dominance of late-flowering species.

Clonality

Enhanced recruitment among clonal species in our analyses is congruent with previous findings in restored calcareous grasslands (Pywell *et al*. 2003) and may result from an increased ability to exploit localized resources following colonization (Cornelissen *et al*. 2003). Allocation towards vegetative reproduction may constrain seedling recruitment among clonal species in natural populations (Olejniczak 2001). Recruitment from seed is believed to be most limited among clonal species with widely dispersed stems indicative of the guerilla growth form than among phalanx species with densely spaced stems, apparently because guerilla species are even less reliant upon sexual reproduction given their ability to disperse intermediate distances vegetatively (Eriksson 1989). Among the species with the highest recruitment rates in this study were phalanx-form clonal species such as *Helianthus maximiliani*, *H. mollis,* and *Monarda fistulosa,* which supports the assertion that recruitment is less strongly limited among phalanx-form clonal species. High recruitment rates of these clonal species and the capacity of clonal species to exploit local resources supports the suggestion of Farnsworth (2007) that land managers adopt more intensive practices to inhibit competitive exclusion of non-clonal species.

Flowering duration

Although flowering duration has been found to influence recruitment in other plant communities (Lake and Leishmann 2004, Moretti and Legg 2009), the underlying cause of this phenomena is not at all clear. Poor recruitment among tallgrass prairie species with short flowering durations

(Fig. 4c-d) may result if seeds sown into restorations have low viability due to pollen limitation in the fragmented populations from which they are harvested. Longer flower duration increases the probability of visitation by pollinators in pollen limited habitats (Kilkenny and Galloway 2008). Pollen limitation has been identified as a constraint on fecundity among remnant populations in the highly fragmented tallgrass prairie landscape (Wagenius 2006), and experimental manipulations that restrict pollinator visitation of native prairie species result in decreased seed viability (Reed 2002). If pollen limitation is common in the fragmented tallgrass prairie, then longer flowering duration may result in greater likelihood of pollination and increased seed viability in the remnants from which seeds for restoration are harvested, and ultimately enhanced recruitment in the restorations in which these seeds are sown. While empirical evidence of pollen limitation has been demonstrated for few species in the tallgrass community, if this phenomenon is widespread, it could explain the poor recruitment of seeds produced by species with short flowering durations. Given that restoration practitioners generally prefer to use local ecotype seed (McKay *et al.* 2005) that is often allocated from isolated prairie remnants, further research is needed to understand the effects of pollen limitation on the viability of seed harvested from these small and fragmented populations.

The low recruitment observed among species with short flower durations may also be influenced by a relationship between flower duration and range size. Given that flowering time was measured using published values for the number of months in which species flower, this measure may be partially influenced by phenological variation across photoperiod and precipitation gradients for species with expansive ranges (Murray *et al*. 2002). Range size has been positively correlated with local abundance in naturally occurring communities (Eriksson and Jakobsson 1998, Farnsworth 2007), though the implication of this relationship for

recruitment in restorations requires further exploration. Future analyses using field measurements of flowering duration and examining the effect of geographical range could clarify the role of this trait for recruitment.

Additional traits

Although analysis of growth form did not reveal significant differences between the recruitment of grasses and forbs, our findings confirm the assertion of restoration practitioners (Weber 1999) that dominant C_4 grass species exhibit high recruitment rates. A Wilcoxon rank-sum test demonstrated that C_4 grasses had higher mean presence than C_3 grasses (W=79; P<0.05), likely due to the increased efficiency of C_4 photosynthesis in the warm and drought prone conditions of the tallgrass region. The native C_3 grass component of prairie diversity is often overlooked, and efforts should be made to increase the inclusion and recruitment of these species in restorations.

We expected that annual and biennial species would excel given the disturbed conditions of many prairie restorations experiments, and although the commonly sown biennial *Rudbeckia hirta* (blackeyed Susan) and the annual *Chamaecrista fasciculata* (partridge pea) were among the most successful species, overall recruitment of annual and biennial species was not statistically different from perennials. Given that annual species often have considerable seed bank longevity (Venable and Brown 1988), low initial recruitment among some short lived species may be overcome by temporal dispersal should more favorable conditions for germination arise.

Our analyses did not demonstrate a significant relationship between leaf area and recruitment despite the potential advantages of various positions on the leaf area spectrum. Or rather, it is possible that the counterbalancing benefits of increased photosynthetic capacity among large leaves and increased drought tolerance among small leaves (Weiher *et al*. 1999, Westoby *et al*.

2002) precluded any definitive advantage for a specific range of leaf sizes. The effect of leaf area is likely more decisive in environments where either light or moisture limitations unambiguously constrain recruitment.

While nitrogen limitation is considered widespread in terrestrial plant communities (Vitousek and Haworth 1991), excess fertility can favor invasive species at the expense of desired natives, prompting the development of carbon amendment strategies to decrease local soil nitrogen concentrations in some tallgrass restorations (Averett *et al.* 2004). Nitrogen fixation was not retained in our statistical models, likely because the benefits of this trait are contingent upon local nutrient limitations, though Wilcoxon rank-sum tests did demonstrate a significantly higher mean presence (W=15,413; $P<0.05$) among nitrogen-fixers. However, this apparent effect on recruitment likely results from significantly increased seed mass relative to non nitrogen-fixing species (W=14,465; $P<0.0001$). Similar patterns of increased seed mass associated with nitrogen fixation have been found among species colonizing floodplains (Walker *et al*. 2006).

Restoration implications

A greater understanding of how plant traits influence community assembly has considerable potential to facilitate ecosystem restoration and management (Walker *et al*. 2006). In this study we have established a foundation for future research through the identification of key plant traits that influence recruitment in grassland restorations. The synthesis of data from numerous studies illuminates trait-based recruitment patterns that emerge across the varied environmental contexts of the tallgrass region, though further research is needed to develop greater predictive capabilities and integrate these findings into management practice. While trait-based analyses may never generate an explicit recipe for ecological restoration (Kirkman *et al*. 2004, Brudvig

and Mabry 2008), research that examines interactions between plant traits, seeding densities, niche requirements, and the timing, duration, and intensity of prescribed disturbances can make a substantial contribution towards refining management practices for the restoration of high diversity plant communities.

While some species are certainly limited by propagule availability, it is costly to assume that recruitment limitations will be overcome through increased seeding rates alone. Species with consistently low recruitment may be limited by stringent niche requirements rather than seed limitations or static competitive inferiority. Accordingly, future research should examine the relationship between fertility, soil moisture, and light requirements of species sown into restorations to determine if traits associated with poor recruitment are indicative of narrow resource requirements. Interspecific competition also limits restored diversity, and awareness of trait-based competitive hierarchies can guide the spatial separation of species with disparate competitive abilities. Prescribed disturbances may alter these competitive hierarchies (Suding and Goldberg 2001) while also changing abiotic conditions that limit recruitment, which elicits the potential benefits of investigating interactions between traits and disturbance in the context of restoration. In addition, filters regulating long term persistence can further restrict diversity (Turnbull *et al*. 2000), even if initial recruitment largely shapes community structure (Weiher and Keddy 1995, Kitajima and Tilman 1996). Improved long term monitoring of restorations could enhance our understanding of how traits affect persistence and community composition.

CONCLUSIONS

Trait-based analysis provides a unique perspective for interpreting patterns of diversity in plant communities. Extensive compilation of restoration datasets, in which dispersal limitations are negated through seed addition, provides an ideal format for discerning prevalent effects of traits on recruitment in grasslands. Our analyses indicate that recruitment is limited by small seed mass, short height, early flowering time, and short flowering durations, while intermediate seed mass, moderately tall height, mid to late season flowering time, increased flowering duration, and clonal growth are advantageous for recruitment. Given the variance in recruitment success associated with particular trait values, it cannot be asserted that possession of any given trait assures successful recruitment. Rather, advantageous traits set a high upper bound on recruitment potential, while disadvantageous traits may severely restrict recruitment. Many traits vary independently, and recruitment potential is greatest when multiple beneficial traits act in concert.

Through the synthesis of data, this study has illuminated trait-based recruitment patterns relevant across the varied abiotic contexts of the tallgrass region. It is our hope this study will prompt further research to enhance the understanding of causal factors underlying trait-based recruitment and integrate this knowledge into restoration practice. These objectives will be facilitated through enhanced accessibility to high quality trait data made possible by the ongoing development of comprehensive trait databases for the North American flora. Advancement of trait-based research holds great promise for the restoration of degraded ecosystems.

Table 1 Plant traits, trait classes, and data sources for each trait analyzed

Trait	Trait Classes	Data Source
Growth Form	Graminoid, Forb	McGregor *et al*. 1986
Lifespan	Annual, Biennial, Perennial	McGregor *et al*. 1986
Photosynthetic Pathway	C3, C4	Freeman 2002
Seed Mass	Continuous	Liu *et al*. 2008
Clonality	Binary	McGregor *et al*. 1986
Nitrogen Fixation	Binary	Freeman 2002
Flower Time	Peak flowering month	McGregor *et al*. 1986
Flower Duration	Number of flowering days	McGregor *et al*. 1986
Plant Height	Continuous	McGregor *et al*. 1986
Leaf Area	Continuous	McGregor *et al*. 1986

Table 2 Author and source journal or organization from which recruitment data was acquired, year of seeding, study location, and the number of datasets obtained from each source

Author	Source	Year	Location	Datasets
Aschenbach 2006	*Ecological Restoration*	1999	Paola, KS	1
Baer *et al*. 2003	*Ecology*	1998	Manhattan, KS	1
Berg 1990	*12th N. Am. Prairie Conf.*	1987	Woodward, OK	1
Bragg & Sutherland 1988	*11th N. Am. Prairie Conf.*	1975	Omaha, NE	1
Dickson & Busby 2009	*Restoration Ecology*	2001	Lawrence, KS	2
Foster & Dickson 2004	*Ecology*	2000	Lawrence, KS	1
Hemsath, Unpublished	U. of Northern Iowa	2005, 06	Cedar Falls, IA	2
Howe 1994	*Ecological Applications*	1986	Viola, WI	1
Howe & Brown 2000	*Ecological Applications*	1997	Viola, WI	3
Barzen, Unpublished	International Crane Foundation	1990-96	Baraboo, WI	6
Kindscher & Fraser 2007	*Ecological Restoration*	1996	Overland Park, KS	2
Long & Kindscher 2007	*Ecological Restoration*	2006	Lawrence, KS	4
Long & Kindscher 2007	*Ecological Restoration*	2006	Williamsburg, MO	1
Martin & Wilsey 2006	*Journal of Applied Ecology*	2003, 04	Prairie City, IA	4
Piper et al. 2007	*Restoration Ecology*	2000	Newton, KS	1
Piper, Unpublished	Bethel College	2007	Newton, KS	5
Stevens *et al*. 2004	*Journal of Ecology*	1998	Linesville, PA	1
Tillman 1997	*Ecology*	1992	Cedar Creek, MN	1
Williams *et al*. 2007	*Restoration Ecology*	1999	Cedar Falls, IA	4
Williams & Smith 2007a	Iowa DOT internal report	2004	Cedar Falls, IA	4
Williams & Smith 2007b	Iowa DOT internal report	2004	Cedar Falls, IA	3
Williams & Smith 2007c	Iowa DOT internal report	2004	Cedar Falls, IA	3
Zimmerman & Schwarzmeier 1976	*5th N. Am. Prairie Conf.*	1974, 76	Madison, WI	2

Table 3 The 190 species for which recruitment data were obtained, with seed mass in parenthesis reported in mg.

Achillea millefolium (0.20)	Dalea candida (1.30)	Liatris ligulistylis (1.61)	Rosa carolina (13.18)
Agastache foeniculum (0.30)	Dalea purpurea (3.20)	Liatris punctata (4.66)	Rudbeckia hirta (0.35)
Allium canadense (8.90)	Dalea villosa (1.89)	Liatris pycnostachya (1.90)	Rudbeckia subtomentosa (0.94)
Allium cernuum (3.85)	Danthonia spicata (0.89)	Liatris spicata (2.90)	Ruellia humilis (3.02)
Allium stellatum (1.89)	Desmanthus illinoensis (6.00)	Lithospermum caroliniense (5.65)	Salvia azurea (3.41)
Amorpha canescens (2.00)	Desmodium canadense (5.10)	Lobelia cardinalis (0.04)	Schizachyrium scoparium (1.50)
Andropogon gerardii (2.40)	Desmodium glutinosum (33.75)	Lobelia siphilitica (0.04)	Scirpus atrovirens (0.05)
Anemone canadensis (2.26)	Desmodium illinoense (6.60)	Lobelia spicata (0.03)	Senna marilandica (22.00)
Anemone cylindrica (1.30)	Dodecatheon meadia (0.23)	Lomatium foeniculaceum (6.34)	Silphium integrifolium (30.65)
Antennaria neglecta (0.08)	Echinacea angustifolia (2.60)	Lupinus perennis (22.10)	Silphium laciniatum (78.05)
Antennaria plantaginifolia (0.09)	Echinacea pallida (5.66)	Lysimachia quadriflora (0.28)	Silphium terebinthinaceum (28.35)
Apocynum cannabinum (1.10)	Echinacea purpurea (2.42)	Mimosa nuttallii (12.50)	Sisyrinchium campestre (0.46)
Arabis lyrata (0.18)	Elymus canadensis (4.40)	Mimulus ringens (0.03)	Solidago canadensis (0.11)
Aristida basiramea (0.39)	Elymus virginicus (4.94)	Monarda fistulosa (0.40)	Solidago gigantea (0.22)
Arnoglossum atriplicifolium (2.67)	Eryngium yuccifolium (3.83)	Monarda punctata (0.30)	Solidago missouriensis (0.33)
Artemisia ludoviciana (0.14)	Eupatoriadelphus maculatus (0.28)	Napaea dioica (6.35)	Solidago nemoralis (0.30)
Asclepias incarnata (3.65)	Eupatorium altissimum (1.81)	Oenothera biennis (0.40)	Solidago speciosa (0.30)
Asclepias sullivantii (4.70)	Euphorbia corollata (3.79)	Oenothera macrocarpa (5.13)	Sorghastrum nutans (2.00)
Asclepias syriaca (7.07)	Euthamia graminifolia (0.08)	Oligoneuron album (0.47)	Spartina pectinata (2.09)
Asclepias tuberosa (6.80)	Gaillardia pulchella (1.70)	Oligoneuron rigidum (0.90)	Sporobolus compositus (0.60)
Asclepias verticillata (2.20)	Gaura mollis (11.31)	Opuntia humifusa (29.99)	Sporobolus cryptandrus (0.10)
Asclepias viridis (6.62)	Gentiana alba (0.21)	Packera paupercula (0.26)	Sporobolus heterolepis (0.19)
Astragalus canadensis (2.00)	Gentiana andrewsii (0.06)	Packera plattensis (0.35)	Symphyotrichum ericoides (0.10)
Baptisia alba (16.42)	Gentianopsis crinita (0.06)	Panicum virgatum (1.30)	Symphyotrichum laeve (0.31)
Baptisia australis (18.00)	Geum triflorum (1.59)	Parthenium integrifolium (3.08)	Symphyotrichum novae-angliae (0.40)
Baptisia bracteata (11.50)	Helenium autumnale (0.50)	Pascopyrum smithii (2.71)	Symphyotrichum oblongifolium (0.56)
Bidens cernua (2.90)	Helianthemum canadense (0.53)	Paspalum setaceum (0.98)	Symphyotrichum oolentangiense (0.17)
Bidens frondosa (3.91)	Helianthus grosseserratus (1.97)	Pedicularis canadensis (0.87)	Symphyotrichum pilosum (0.65)
Boltonia asteroides (0.10)	Helianthus maximiliani (2.00)	Penstemon cobaea (3.07)	Symphyotrichum praealtum (0.22)
Bouteloua curtipendula (1.30)	Helianthus mollis (4.70)	Penstemon digitalis (0.22)	Symphyotrichum sericeum (1.09)
Bouteloua gracilis (0.43)	Helianthus occidentalis (2.30)	Penstemon gracilis (0.06)	Tephrosia virginiana (11.11)
Bouteloua hirsuta (0.44)	Helianthus pauciflorus (7.77)	Penstemon grandiflorus (1.80)	Thalictrum dasycarpum (2.27)
Brickellia eupatorioides (0.94)	Heliopsis helianthoides (4.15)	Phlox pilosa (1.49)	Tradescantia bracteata (2.86)
Buchnera americana (0.02)	Hesperostipa spartea (3.20)	Polygala polygama (1.64)	Tradescantia ohiensis (3.66)
Calamagrostis canadensis (0.10)	Heuchera richardsonii (0.06)	Polygonum convolvulus (6.90)	Triodanis perfoliata (0.03)
Callirhoe involucrata (5.60)	Hieracium canadense (0.20)	Polytaenia nuttallii (5.80)	Tripsacum dactyloides (61.14)
Callirhoe triangulata (5.34)	Hieracium longipilum (0.31)	Potentilla arguta (0.15)	Veratrum virginicum (3.15)
Camassia scilloides (6.05)	Hierochloe odorata (0.45)	Prenanthes racemosa (2.02)	Verbena hastata (0.23)
Campanula rotundifolia (0.06)	Hypericum ascyron (0.12)	Pseudognaphalium obtusifolium (0.04)	Verbena stricta (1.00)
Carex annectens (0.43)	Ionactis linariifolius (0.81)	Psoralidium tenuiflorum (26.16)	Verbena urticifolia (0.46)
Castilleja sessiliflora (0.18)	Iris virginica (21.81)	Pulsatilla patens (1.96)	Vernonia fasciculata (1.18)
Ceanothus americanus (3.49)	Koeleria macrantha (0.30)	Pycnanthemum tenuifolium (0.07)	Veronicastrum virginicum (0.07)
Ceanothus herbaceus (4.05)	Krigia virginica (0.42)	Pycnanthemum virginianum (0.14)	Viola pedata (0.93)
Chamaecrista fasciculata (8.40)	Lathyrus venosus (32.76)	Ranunculus fascicularis (2.24)	Viola pedatifida (1.01)
Chelone glabra (0.50)	Lespedeza capitata (2.90)	Ranunculus rhomboideus (1.42)	Zizia aptera (1.52)
Coreopsis lanceolata (1.30)	Lespedeza virginica (1.91)	Ratibida columnifera (0.92)	Zizia aurea (2.35)
Coreopsis palmata (1.99)	Liatris aspera (2.10)	Ratibida pinnata (0.87)	
Coreopsis tinctoria (0.30)	Liatris cylindracea (3.26)	Rosa arkansana (12.9)	

Table 4 Traits retained as main effects in the logistic regression model for recruitment probability based on species presence. Estimates are parameters for predicting the influence of traits on the log odds ratio.

	Mean Presence			
Predictor	Parameter Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	-1.089	0.193	-5.653	1.58E-08
Seed Mass	0.469	0.087	5.390	7.05E-08
Flwr Duration (90)	0.289	0.142	2.031	4.22E-02
Flwr Duration (120)	0.517	0.151	3.418	6.30E-04
Flwr Duration (150)	0.479	0.209	2.288	2.21E-02
Flwr Time (Jun)	0.889	0.183	4.870	1.12E-06
Flwr Time (Jul)	1.906	0.213	8.969	2.00E-16
Flwr Time (Aug)	1.241	0.209	5.942	2.81E-09
Flwr Time (Sep)	1.383	0.216	6.395	1.61E-10
Height	0.005	0.002	2.539	1.11E-02
Clonality	0.589	0.114	5.174	2.30E-07

Null deviance = 807.03, d.f.= 188; Residual deviance = 626.06, d.f.= 177; AIC = 930.7

Table 5 Trait interaction model variants, exhibiting which interactions were entered into the model, which traits or trait category interactions were significant in each model, and the AIC score, degrees of freedom, and null minus residual deviance in each model. All significant interactions were positive.

Model Interactions	Significant Terms (p<0.05)	AIC	d.f.	null-res.dev.
FlwrTme x FlwrDur	(Jul x 90d, 120d,150d)(Aug x 120d)	858.4	26	283
FlwrTme x Height	(Jun, Jul x Height)			
Sd Mass x Height	(Sd Mass x Height)			
FlwrTme x FlwrDur	(Jul x 90d, 120d)	877.5	28	268
Sd Mass x FlwrDur	(Sd Mass x 90d, 120d,150d)			
Sd Mass x FlwrTme	(Sd Mass x Aug)			
FlwrTme x FlwrDur	(Jul x 90d, 120d)	886.3	25	253
Sd Mass x FlwrDur	(Sd Mass x 90d, 120d,150d)			

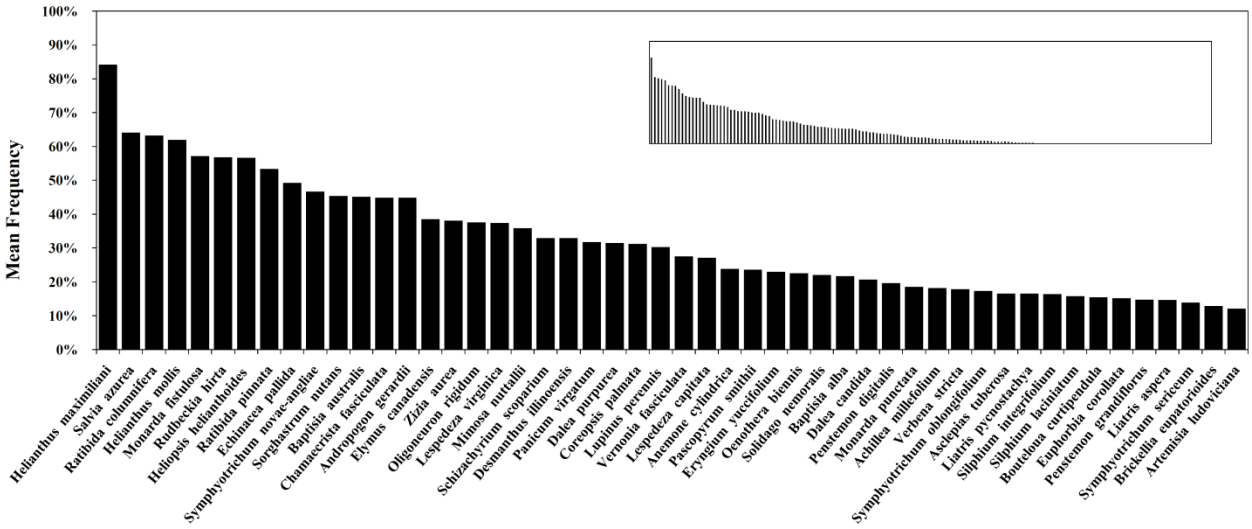

Figure 1 The 50 species with the highest mean frequency values in descending order. The inset displays the full distribution of mean species frequency (n=162) across all studies.

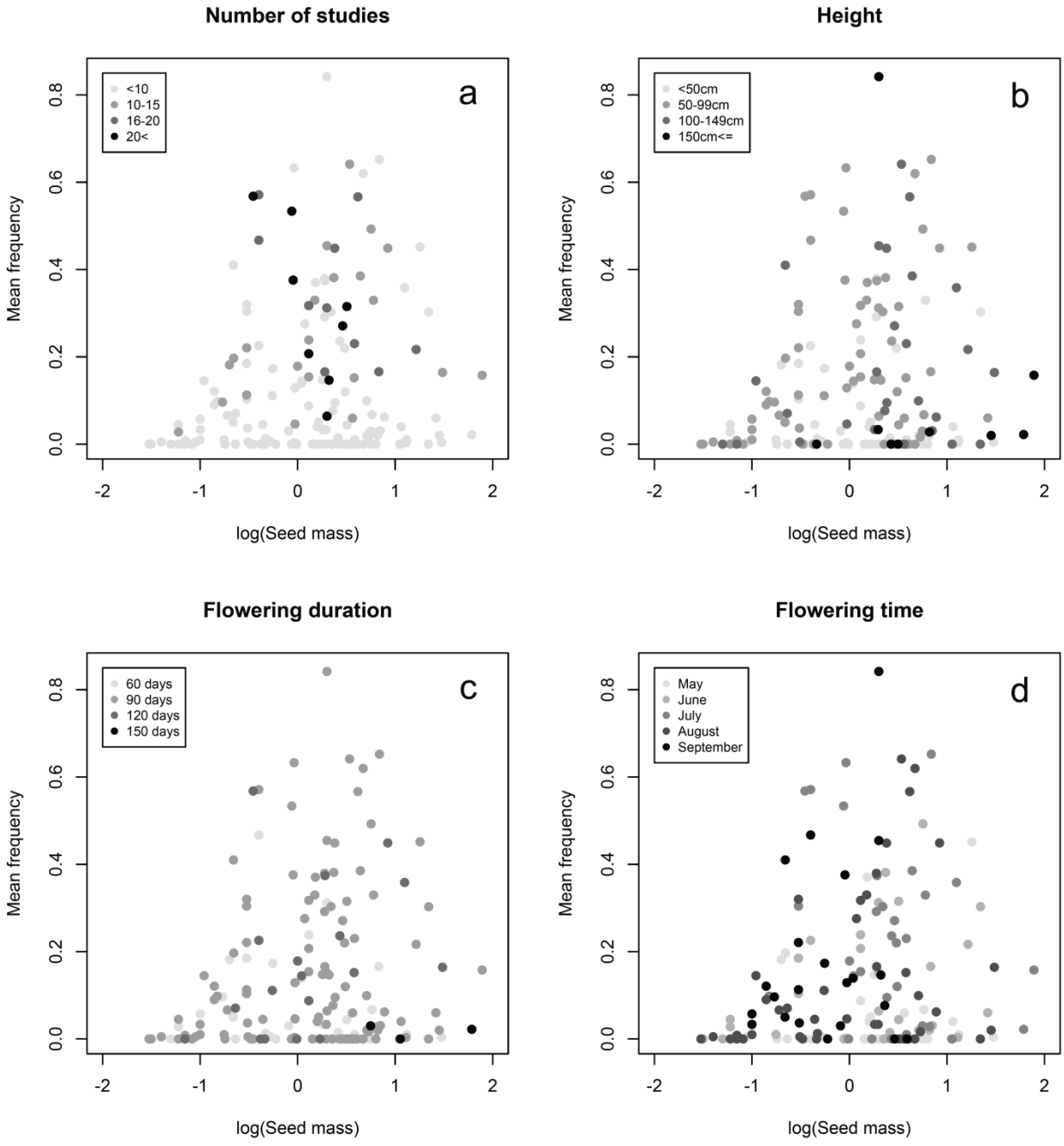

Figure 2 Mean frequency per species (n=162) as a function of Log_{10} seed mass (mg). In each panel species are classified according to values for a.) the numbers of studies used to calculate mean frequency, b.) height (cm), c.) flowering duration, and d.) flowering time.

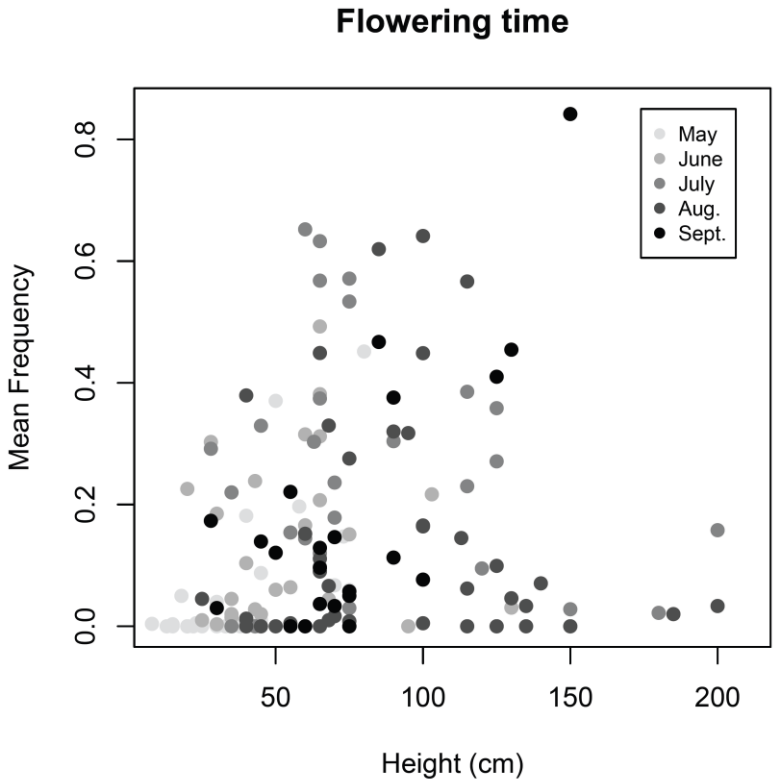

Figure 3 Mean frequency per species (n=162) as a function of height (cm), with species classified according to values for flowering time.

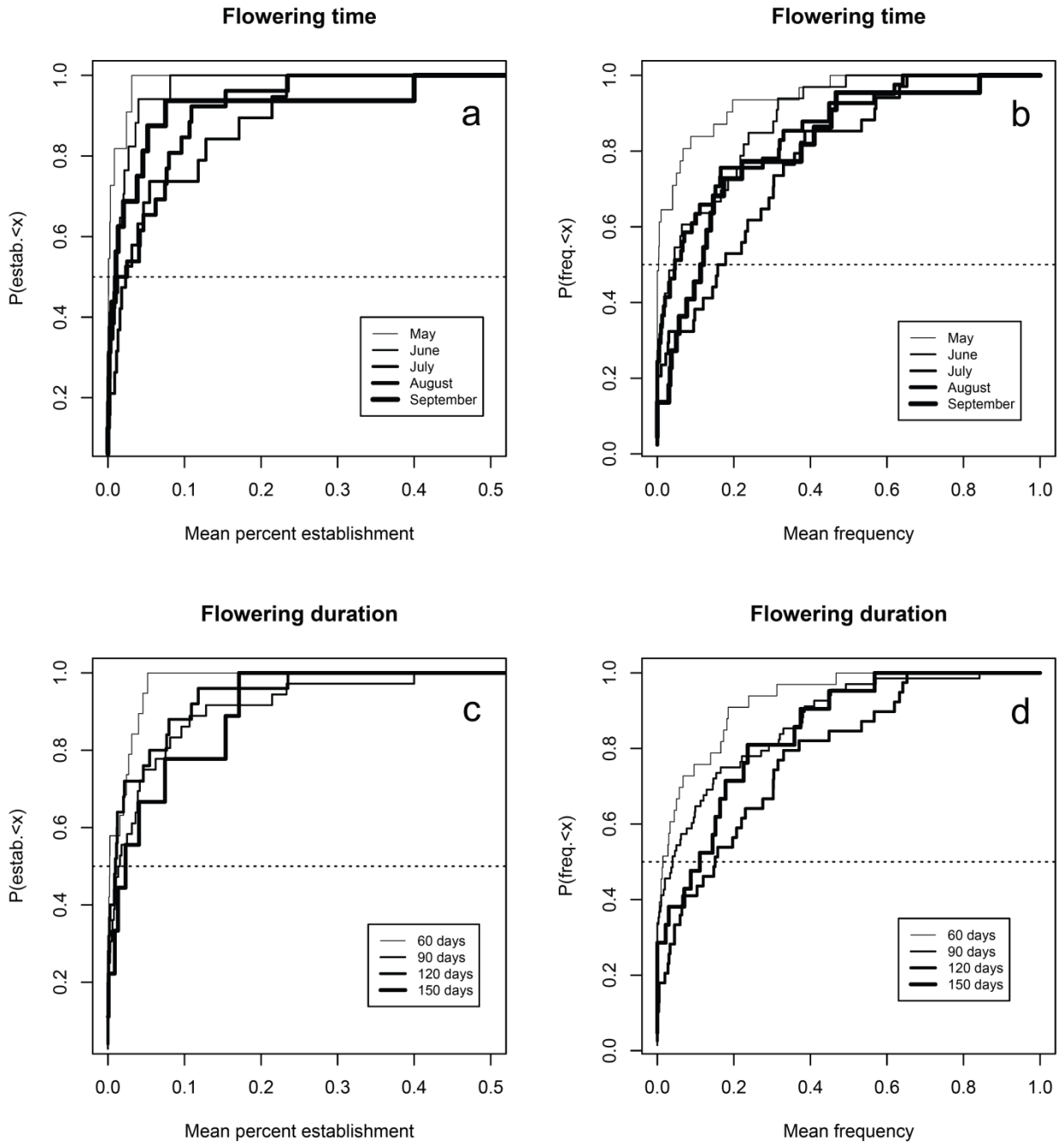

Figure 4 Cumulative distribution function of mean percent establishment (a,c) and mean frequency (b,d) for trait classes of flowering time (a,b) and flowering duration (c,d). P(estab.<x) and P(freq.<x) represent the probability that a species in a given trait class will assume a value less than or equal to x for mean percent establishment or mean frequency, respectively. Median values are designated by a dashed line, which indicates that 50% of species in a given trait class will have recruitment rates lower than the corresponding value on the x-axis. The x-axis value corresponding with the point at which the distribution function reaches 1.0 indicates the highest mean recruitment value observed among species in a given trait class.

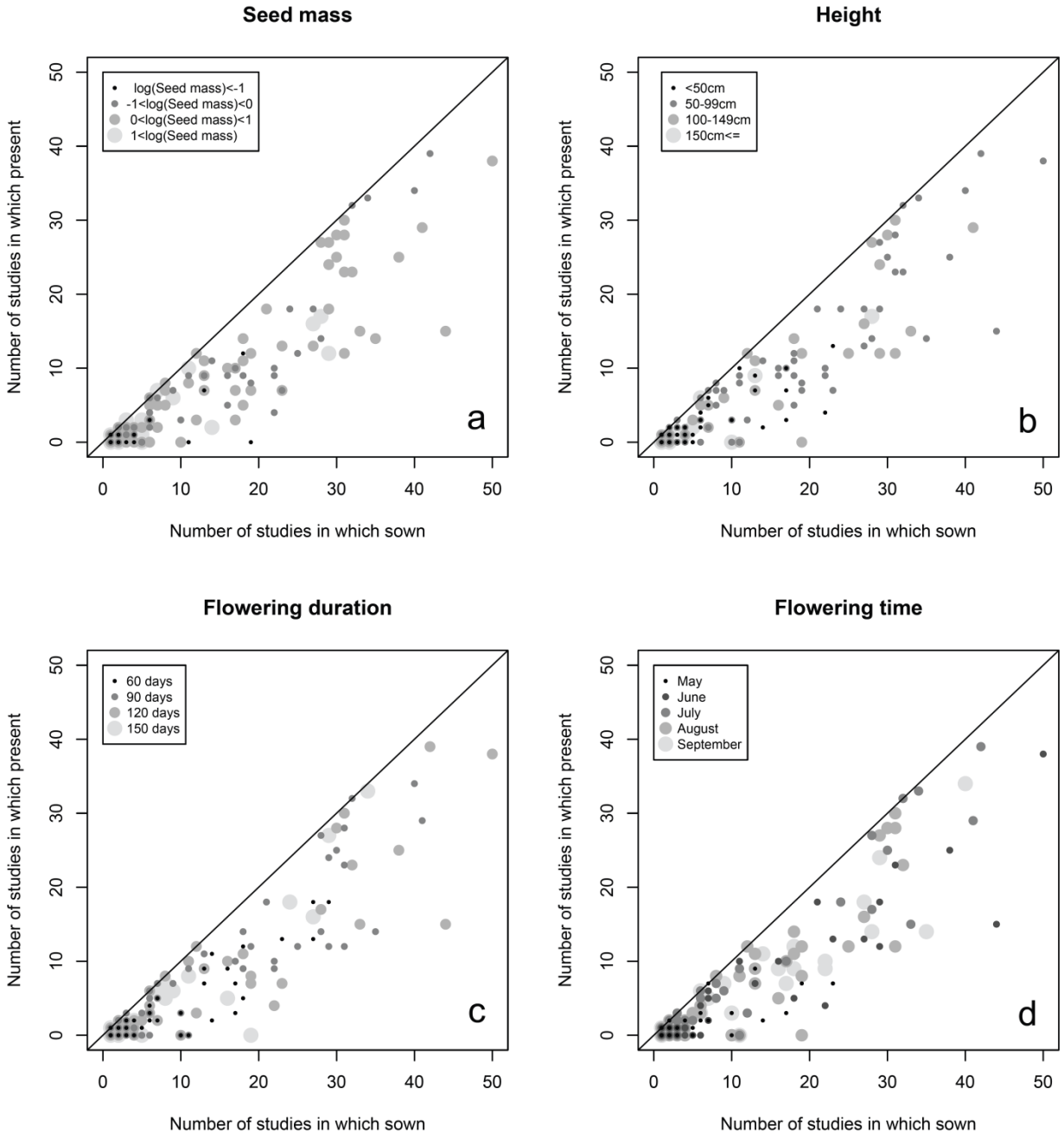

Figure 5 Mean presence displayed as the number of studies in which a species was present as a function of the number of studies in which the species was sown. Each point represents individual species (n=190) classified according to values for a.) Log_{10} seed mass (mg), b.) height (cm), c.) flowering duration and d.) flowering time. Species sown in the same number of studies that have equal recruitment can be distinguished if they have different values for a given trait.

Chapter 3

Interseeding and heterogeneous disturbances increase native recruitment and diversity in prairie restorations

CHAPTER SUMMARY

The need for restoration of the tallgrass prairie biome is marked by critical declines of characteristic flora and fauna. Though restorations rarely approximate the diverse flora of remnant prairies due to poor native forb establishment, methods of enhancing forb diversity in existing restorations have been poorly investigated. We examine effects of multiple disturbance regimes on recruitment of native forbs sown into species-poor native grassland restorations at three tallgrass prairie sites and evaluate the potential for mosaic disturbance management to increase floral and structural heterogeneity. Native forbs were sown into plots that were either undisturbed, summer burned, or subjected to one of the following disturbances in addition to summer burning: broad-spectrum herbicide, shallow disking, mowing, or annual spring burning. Native richness increased in response to sowing without disturbance, though disturbances further enhanced recruitment. Light availability was a strong predictor of recruitment, and the benefit of increased disturbance intensity was contingent upon the extent to which productivity limited light availability at each location. Initial application of herbicide had the adverse effect of promoting colonization by exotic species when abundant in the surrounding landscape. We found significant differences in native forb community composition among treatments, but no singular treatment resulted in decisively superior establishment of sown species. These findings, together with the variable structural requirements of grassland fauna, indicate that heterogeneous disturbance regimes within a single restoration site can benefit native forb establishment and enhance wildlife habitat value.

INTRODUCTION

It is estimated that as little as 1% of the 162 million hectares of native tallgrass prairie that existed prior that to European settlement remains intact, which represents the largest decline of any major North American ecosystem (Samson and Knopf 1994). As a result of this dramatic loss of habitat, grassland birds have experienced more precipitous declines than any other avian assemblage in North America (Sauer *et al.* 2008) and many grassland insects have declined due to host-plant rarity (Reis *et al.* 2001, Vogel *et al.* 2007, Nemec and Bragg 2008). Isolated prairie remnants in highly fragmented landscapes are inadequate to support long-term persistence for many endemic species of plants (Maschinksi 2006), insects (Schultz and Crone 2005), and birds (Herkert 1994), thus large-scale restoration is necessary to provide critical habitat for declining grassland flora and fauna (Herkert *et al.* 2003, Olechnowski *et al.* 2009).

Despite the tremendous need for restoration of this imperiled ecosystem, restored prairies rarely approach the floral diversity of remnants due to poor forb establishment (Kindscher and Tieszen 1998, Martin *et al.* 2005, Polley *et al.* 2005). Consequently, restorations also support lower faunal diversity than remnants (Brand and Dunn 1998, Shepherd and Debinski 2005). Restoration of dominant warm-season grasses is readily achieved and may be adequate to attain objectives like erosion control (Baer *et al.* 2002), but restoration of sub-dominant species may be necessary to maintain restored ecosystem functions such as efficient carbon sequestration and nutrient cycling in response to future environmental changes (Naeem 2006). While grasses are considerably more abundant even in remnant prairies, forbs comprise the vast majority of richness in these communities (Weaver 1934, Collins *et al.* 1998). Accordingly, efforts to enrich prairie restorations should concentrate on enhancing forb diversity.

Forb establishment in restorations is often inhibited by the dominance of warm-season grasses (Kindscher and Tieszen 1998, Collins 1992, Copeland *et al.* 2002). Specifically, recruitment can be limited by poor light availability due to high productivity of dominant grasses and substantial litter accumulation (Knapp and Seastedt 1986, Tilman 1993, Facelli and Facelli 1993). Strategies to increase diversity in new restorations include sowing forbs prior to dominant grasses (Kindscher and Fraser 2000) and increasing the abundance of forbs relative to warm-season grasses in seed mixes (Weber 1999, Dickson and Busby 2009). However, few studies have assessed management practices intended to increase diversity through interseeding forbs into established low diversity restorations. Effective interseeding practices could enhance not only low diversity restorations, but also the native diversity and habitat value of the 2.8 million hectares of low diversity warm-season grass plantings enrolled in the Conservation Reserve Program (CRP) (USDA, 2008). Although the CRP was initiated primarily to prevent soil erosion and improve water quality and is not explicitly a prairie restoration program, CRP plantings provide valuable wildlife habitat in agricultural landscapes (Van Buskirk and Willi 2004). The conservation value of CRP plantings could be significantly enhanced by management practices that increase their floral diversity and structural heterogeneity (Rahmig *et al.* 2009).

In this study we experimentally compare five contrasting managed disturbances applied to warm-season grass stands in conjunction with restorative interseeding to determine which practices most successfully enhance native forb recruitment while limiting invasion by exotic species. We also evaluate whether applying a variety of managed disturbances at the same restoration site (mosaic disturbance management) could be effectively employed to increase the floral and structural heterogeneity of restored grasslands. As a common principle of community ecology, it has been asserted that species coexistence and biodiversity is maximized when the

timing, intensity, frequency, and form of disturbances are spatially and temporally distributed in a heterogeneous fashion across the landscape (Huston 1979). Studies of prairie management have repeatedly suggested that mosaic applications of common practices such as burning, mowing, and grazing could be employed at various scales to generate greater diversity than any single management regime applied homogeneously across a restoration site (Howe 1994a, Davison and Kindscher 1999, Brudvig *et al.* 2007). This is based on the assumption that species differ greatly in their regeneration niches (Grubb 1977) and that applying heterogeneous disturbances increases the niche dimensionality of the habitat (Questad and Foster 2008), thus expanding recruitment opportunities for a greater variety of species. Given that disturbances can influence the availability and quality of establishment niches and alter competitive hierarchies in plant communities (Suding and Goldberg 2001), application of mosaic disturbances in conjunction with interseeding could create distinct species assemblages within patches subjected to each disturbance regime. Recent landscape-scale studies of patch-burn grazing in rangelands have shown that heterogeneous disturbances can enhance diversity in native plant communities, while also increasing faunal diversity by concurrently providing habitat for species that are disturbance-dependent and disturbance-sensitive (Fuhlendorf *et al.* 2009). If multiple viable strategies exist for forb enrichment of established warm-season grasslands, then mosaic disturbances and interseeding could be conducted in tandem to meet the dual objectives of enhancing plant diversity and optimizing the value of wildlife habitat.

Given that warm-season grasses can inhibit forb colonization, disturbance-generated gaps are often necessary to create suitable conditions for germination and seedling survival (Williams *et al.* 2007). Prescribed fire prior to sowing may enhance colonization by removing accumulated thatch, improving seed/soil contact, and increasing resource availability. Timing of burns can

also affect community composition in tallgrass prairie. Prescribed burns during the historical peak of natural lightning fires in July-August (Bragg 1982) exhibit greater variation in intensity and structural patchiness relative to spring burns (Howe 1999). Summer burns also may reduce warm-season grass dominance by damaging tissues during their peak growth period, thus stimulating growth of early-season forbs and increasing seedling recruitment (Glenn-Lewin *et al.* 1990, Howe 1994a, 1994b, Copeland *et al.* 2002).

In conjunction with prescribed burning prior to interseeding, additional disturbances may further enhance forb establishment. Warm-season grass roots occur in dense mats just below the soil surface, causing such high absorption of soil water that colonization can be inhibited on apparently bare areas (Weaver 1934). Disturbing grass roots by shallow disking may facilitate forb establishment in grassland restorations (Pywell *et al.* 2002), and disking after prescribed burns has long been promoted to stimulate forb cover for wildlife in CRP plantings (Buckner and Landers 1979). Since grazing can be logistically impractical for many restorations of small acreage (Davison and Kindscher 1999), mowing is often used to decrease live biomass of warm-season grasses (Collins *et al.* 1998). Mowing throughout the growing season after interseeding has been shown to promote native forb establishment in low-diversity prairies (Williams *et al.* 2007), but has not previously been compared directly with other interseeding approaches. While spring burning is frequently prescribed to maintain tallgrass prairies, increased dominance of warm-season grasses in response to this practice (Howe 1994a, Collins *et al.* 1998) appears incongruent with post-interseeding management of forb enrichment projects. However, if poor light availability due to thatch accumulation more severely limits forb establishment than the dominance of warm-season grasses per se, then annual spring burns in the years following seed addition could potentially enhance recruitment. Since the objective of interseeding is to enhance

recruitment and diversity while retaining established native vegetation (Williams *et al.* 2007), widespread use of broad-spectrum herbicide is inadvisable before interseeding. However, if elimination of existing vegetation were necessary for effective forb establishment in productive grasslands, then spraying and subsequently seeding small patches throughout a larger landscape could be a viable forb enrichment strategy.

We hypothesize that interseeding forbs into established stands of native warm-season grasses will increase native forb diversity. Further, we hypothesize that managed disturbance treatments which most effectively increase availability of open microsites and light will result in the greatest level of native forb establishment and diversity. Because disturbances that promote native forb recruitment may also create establishment opportunities for exotic species, we hypothesize that recruitment of exotics would also increase in response to disturbance and be highest following the elimination of resident vegetation by broad-spectrum herbicide. Finally, consistent with the mosaic disturbance concept, we predicted that native forb composition will vary significantly more among than within disturbance treatments because different species would be favored by the specific type, timing, and intensity of disturbance associated with each management regime.

METHODS

Study areas

We conducted this study at the Prairie Fork Conservation Area (Prairie Fork) in central Missouri (38°N, 91°W) and on two tracts of the University of Kansas Field Station in North Eastern Kansas (39°N, 91°W): the Nelson Environmental Studies Area (Nelson) and the McColl Nature

Reserve (McColl). The humid continental climate of the prairie-forest ecotone region in which these research areas are located is characterized by extreme seasonal temperature fluctuations, with minimum temperatures in winter as low as -29°C and maximum summer temperatures as high as 43°C. While recorded temperature extremes are approximately equivalent at all locations, the mean annual temperature at Nelson and McColl (13.3°C) is slightly higher than at Prairie Fork (12.3°C). Seasonal distribution of precipitation peaks unimodally in May through June for all locations, though mean annual precipitation at Nelson and McColl (940mm) is less than at Prairie Fork (995mm). Study locations within each research area were upland warm-season grass plantings characterized by big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), with the experiments positioned in sites that exhibited maximal homogeneity of vegetative composition and structure, topography, and soil conditions. Each site had previously been in agricultural production, and warm-season grasses were planted in 1957 at Nelson, 1987 at McColl, and 1988 at Prairie Fork.

These sites exhibited characteristic native species richness for warm-season CRP plantings. Pre-treatment native species richness within a sampling area of 400 square meters was 37 species at Nelson and 38 species at both Prairie Fork and McColl. These values are nearly equivalent to the average native richness reported by Jog *et al.* (2006) from a survey of an equal sampling area at each of 20 CRP fields (39 species), and characteristically low compared to the average native richness reported by their survey of 20 nearby remnant prairies (70 species) in Eastern KS.

Treatment applications

In mid-April 2005 we established an 8 x 4 grid of 32 permanently marked $4m^2$ plots separated by 3m buffer strips at both the Nelson and Prairie Fork sites. Using a completely randomized design

we established six experimental treatments (n=5), all of which were designated to be sown with prairie forbs, but which differed in the form of disturbance applied. Plots were either undisturbed, summer burned, or received one of the following treatments *in addition* to summer burning: shallow disking, mowing, annual spring burning, or broad-spectrum herbicide application (Table 1). Hereafter the treatment which was summer burned without additional disturbance will be referred to as "summer burn" and all other disturbance treatments will be referred to by the disturbance conducted in addition to summer burning (i.e. "disking"). In addition to these six treatments, two control plots were established that were neither seeded nor disturbed. At McColl the application of broad-spectrum herbicide was contractually prohibited by enrollment in CRP, so the plot design was modified to comprise a 7 x 4 grid of 28 plots in which we established the other five experimental treatments (n=5) and control plots (n=3).

We designed seed mixes to include 37 native forb species (Table 2) that are characteristic of the regional tallgrass prairie flora, but were absent from sites prior to sowing. To account for variation in viability, we only purchased seeds from single-source accessions with pure live seed (PLS) estimates. We weighed 100 seeds per species to calculate mean seed mass, then weighted that value by PLS estimates to create seed mixes for each plot comprised of equal numbers of viable propagules per species and a cumulative rate of approximately 1,550 seeds/m^2.

In the herbicide plots we sprayed a 5% solution of glyphosate in early July 2005, resulting in complete fatality of resident vegetation. In August 2005, we conducted prescribed burns for all disturbance treatments. Regrowth of vegetation following burns was minimal and generated insufficient litter to impede subsequent seed/soil contact. We conducted disking in November 2005 at an approximate depth of 7 cm using a tractor-mounted disk. In late December 2005, seed mixes were combined with sawdust to facilitate uniform distribution and were hand-broadcast

into all plots except controls. In early July 2006, we used a tractor mounted rotary mower to cut vegetation in mowing treatment plots to 15-20 cm aboveground, which exceeded the height of developing seedlings. Resultant thatch was insufficient to smother seedlings and was not removed. In the annual burn treatment plots we performed prescribed burns during mid-March of 2007 and 2008 when sown native forbs were dormant. Spring burns were not conducted in 2006 because the summer burn in 2005 consumed the litter layer, and at least one growing season is needed for tallgrass prairies to re-accumulate sufficient thatch to effectively burn (Bragg 1982).

Data collection

We sampled vegetation each year in mid-June from 2005 to 2008, thus recording one year of baseline data prior to seed addition for each treatment. We documented presence and visually estimated percent cover of all vascular plant species, bare ground, and thatch in each $4m^2$ plot. Cover within plots was assessed independently for each species such that total cover could exceed 100% to characterize canopy layering. Additionally, we established a permanent $1m^2$ subplot within each plot in which we counted stems for all herbaceous species present. Multiple stems of a given species were recorded as independent occurrences unless we could confirm without disturbing the soil that the stems belonged to the same genet. We acquired current species nomenclature from the PLANTS Database (USDA, NRCS 2010).

We measured Photosynthetically Active Radiation (PAR; $\mu mol\ m^{-2}s^{-1}$) each year in mid July from 2005-2007 using a 0.8-m AccuPAR LP-80 ceptometer (Decagon Devices, Pullman, Washington, USA). PAR was measured to determine the effect of treatments on light availability at the soil surface and to provide a non-destructive measurement of biomass. For each plot we calculated PAR values above and below the canopy based on 4 paired

measurements recorded at approximately 50 cm above the canopy and at the soil surface, inserting the ceptometer probe beneath the litter layer when necessary. All light measurements were recorded at midday under clear sky conditions. Light penetration was expressed as the percentage of PAR above the canopy to reach the soil surface, while biomass is inversely approximated by the percentage of PAR intercepted by the canopy and litter layers.

To directly measure biomass, we collected, dried, and weighed vegetation and thatch within $0.5m^2$ quadrats in July 2005 and at the conclusion of the experiment in July 2008. In 2005 we collected biomass from 10 quadrats per site randomly located within 3m buffer strips between plots and measured dry weight of thatch, graminoids, and forbs in order to quantify pre-treatment levels of biomass at each study location. In 2008 we collected biomass from one $0.5m^2$ quadrat per plot and separately dried and weighed thatch, grass, volunteer forbs, and sown forbs in order to quantify treatment effects on biomass within and among sites.

Statistical analysis

For each sampling period, we used presence data from $4m^2$ plots to determine species richness and stem count data from the $1m^2$ subplots to calculate Shannon diversity (H') and community evenness (*E* calculated as $H/\ln S$). These indices were calculated for sown species, native volunteer species, and exotic species. We analyzed data from the final sampling period for each response variable in order to provide the greatest approximation of long-term treatment effects on community composition, diversity, and structure. We examined effects of site, treatment, and site x treatment interactions on diversity indices, density, biomass, cover, and PAR penetration using two-way analysis of variance (ANOVA). Type IV sums of squares were used to account

for the unbalanced design that resulted from not conducting the glyphosate treatment at McColl. To account for heterogeneous variances of untransformed data, a $Log_{10} + 1$ transformation was applied to biomass data, a square-root transformation was applied to cover and density data, and an arcsine square-root transformation was applied to the proportional data of percent PAR penetration. We performed *a posteriori* multiple comparisons among treatments within each site using Tukey's HSD test (Sokal and Rohlf 1995). Stepwise multiple regressions were used to determine which of the following variables best predict the richness and density of native and exotic species: bare ground, grass cover, grass biomass, thatch cover, thatch biomass, and PAR penetration. Due to inter-correlations among some predictor variables, we determined the extent of collinearity for each multiple regression and assessed acceptable levels using the following criteria: condition index </30, variance inflation </1 / (1-/r^2), and variance proportions not close to one. The preceding analyses were conducted in SPSS 17.0 for Windows (2008).

Comparisons of community composition among treatments were made within each site using Permutational Multivariate Analysis of Variance (PERMANOVA). We used the Sørenson index as the distance measure between sampled communities and conducted separate analyses for total species composition and sown species composition. PERMANOVA tests were conducted in PC-ORD (McCune and Mefford 1999) based on the methods of Anderson (2001) and McArdle and Anderson (2001), with P values for the test statistic (pseudo F value) calculated from 9,999 permutations of stem count relative abundances. We then used relative abundances of sown species to perform ordination of plots within sites using Non-metric Multidimensional Scaling (NMS) with Sørenson distance measures. Lastly, to identify sown species that underlie compositional differences among treatments, we performed Indicator Species Analysis (ISA; Dufrene and Legendre 1997). For each species, ISA assigns an indicator value (*IV*) for treatment

that can range from 0-100% of perfect indication, based on species presence and abundance. Significance of the observed maximum *IV* with respect to treatment was calculated in PC-ORD for each species using a Monte Carlo test with 5,000 iterations.

RESULTS

Light and productivity

Pre-treatment measures demonstrated significant differences in the biomass of grasses, forbs, and thatch among sites (Fig. 1). Baseline PAR measurements within each plot demonstrated that pre-treatment light availability did not vary with the treatment designation of plots ($F = 0.56_{5,68}$ p = 0.72), but was affected by site ($F = 3.88_{2,68}$ p = 0.025). The oldest site, Nelson, exhibited higher light availability and lower grass and thatch biomass than Prairie Fork or McColl, and post-treatment measurements illustrate that this hierarchy persisted throughout the study (Fig. 2).

Treatments had significant effects on final measures of light availability, grass biomass, and thatch biomass across sites (Table 3; Fig. 2). Light availability was consistently higher in glyphosate and spring burn plots and lower in the undisturbed plots (Fig. 2a). Grass biomass only differed significantly among treatments at Prairie Fork, where limited re-colonization after glyphosate application resulted in lower grass biomass than all other treatments (Fig. 2b). Spring burns completely eliminated thatch and were excluded from the two-way ANOVA due to the absence of variance structure. Thatch biomass did not differ significantly among the remaining treatments at Nelson or McColl. At Prairie Fork, low grass productivity in glyphosate plots

decreased thatch accumulation, while mowing effectively decreased thatch relative to undisturbed and summer burned plots (Fig. 2c).

Multiple regression models (Table 4) indicated that light availability and thatch biomass were the strongest determinants of sown species establishment among variables that approximate productivity and structure, with richness and density of sown species demonstrating a positive response to light and a negative response to thatch biomass. Exotic species richness is also most significantly explained by increased light availability, while low grass biomass was the strongest determinant of exotic species density.

Native species establishment

Of the 37 native forb species sown in treatment plots, all 37 species were recorded during the 2006 sampling period and 33 species were still present at varying frequencies in 2008 (Table 2). Sown species were absent from all plots prior to sowing and did not colonize controls over the course of the study. Despite declines in richness and evenness of sown species over the course of the 2006-2008 sampling periods, percent cover of sown species increased as individuals grew larger, and by the conclusion of the study sown species matured sufficiently to indicate probable long-term persistence (Fig. 3e). Total native diversity and richness increased relative to control plots in response to seed addition and disturbance at each site, and sowing without disturbance still significantly increased native richness at the less productive Nelson site (Table 3; Fig 4a-b).

Two-way ANOVAs demonstrated significant effects of site, treatment, and site x treatment interactions on establishment of sown species (Table 3; Fig. 3a-f). Pairwise comparisons demonstrated that sown species richness did not differ significantly among treatments at Nelson ($p > 0.05$), while at both Prairie Fork and McColl the undisturbed treatment resulted in

significantly lower richness than all other disturbance treatments ($p < 0.05$; Fig. 3a). The undisturbed treatment led to significantly higher evenness of sown species than the glyphosate treatment at Nelson and Prairie Fork, but conversely exhibited significantly lower evenness than other seed addition treatments at McColl (Fig. 3b). Density of sown species (Fig. 3d) was lowest in the undisturbed treatment at all sites, with glyphosate resulting in the highest density at the Nelson and Prairie Fork sites where that treatment was conducted. Cover and biomass of sown species were highest in glyphosate plots, and were significantly lower in all other treatments at Nelson (Fig. 3e&f). At McColl, in the absence of the glyphosate treatment, there were no significant differences among treatments in the cover or biomass of sown species.

Exotic species establishment

Richness, density, and cover of exotic species were minimal at Nelson and McColl and did not significantly differ among treatments ($p > 0.05$; Fig. 5a-c). However, each measure of exotic establishment exhibited significant differences among treatments at Prairie Fork, where glyphosate application resulted in a 640% increase in exotic stem density and a 470% increase in exotic cover relative to other treatments due to the proliferation of the exotic legumes black medick (*Medicago lupulina*) and sericea lespedeza (*Lespedeza cuneata*). Although exotic species were not present in plots prior to treatments, species responding to glyphosate application at Prairie Fork were observed to be common in the surrounding landscape.

Community composition

PERMANOVA demonstrated significant differences in the composition of sown species among treatments (Nelson: $F= 3.78_{5,24}$ $p < 0.001$; Prairie Fork: $F= 2.57_{5,24}$ $p < 0.001$; McColl: $F= 2.61_{4,20}$ $p < 0.001$). At each site the undisturbed treatment resulted in a species composition that

was significantly different (p <0.001) than all other treatments. Additionally, at Nelson the glyphosate treatment was significantly different (p <0.05) from all other disturbance treatments and mowing was significantly different than disking (p <0.05). At Prairie Fork the spring burn treatment was significantly different (p <0.05) from all others, and at McColl only the summer burn and annual spring burn treatments had significantly different (p <0.05) community compositions among disturbed treatments. Non-metric multidimensional scaling (NMS) generated two-dimensional ordinations of sown species compositions for all plots within each site. These ordinations visually portray the variation in sown species community composition among treatments (Fig. 6) indicated by PERMANOVA. Expanding analyses of community composition to include all species, rather than solely sown species, yielded the same significant differences among treatments at Nelson and McColl. However, at Prairie Fork, where exotic species colonization was pronounced, the glyphosate treatment had a significantly different (p <0.05) composition from all other treatments when non-sown species were included in analyses.

Indicator Species Analyses (ISA) revealed sown species that significantly indicate treatments at each site, though no species was a significant indicator of the same treatment across sites (Table 5). This illustrates that establishment of certain species is strongly favored by particular treatments, but that the nature of this relationship is highly contingent on site-specific factors. It is noteworthy that in undisturbed plots, five species (*Amorpha canescens*, *Monarda fistulosa*, *Pentstemon digitalis*, *Polytaenia nuttallii,* and *Zizia aurea*) exhibited maximal abundance at the less productive Nelson site, only *Z. aurea* exhibited peak abundance at McColl, and no species exhibited peak abundance in undisturbed plots at Prairie Fork.

DISCUSSION

By conducting experiments at three distinct locations we have identified results with broad implications for grassland restoration, while illustrating that management recommendations are contingent upon site characteristics and restoration objectives. This study demonstrates that interseeding can potentially increase native species richness and diversity in warm-season grass plantings even without disturbance. Disturbance can alter the availability of resources that constrain recruitment, and prescribed disturbances in this study increased light availability and enhanced establishment of sown forbs, especially at more productive sites. However, the severe disturbance of broad-spectrum herbicide application promoted recruitment of exotic species from the surrounding community. Environmental variation among research sites can alter responses of native and exotic species, leading to inconsistent community compositions associated with the same restoration practice conducted at multiple locations. Multiple disturbances applied within a single site could promote heterogeneous composition and structure of vegetation, which could enhance both large scale diversity of plant communities and the critical wildlife habitat value of restorations for declining grassland bird species.

Increased diversity in response to sowing native forbs in this experiment supports previous evidence that diversity in grassland communities is constrained by limited colonization from local seed sources (Zobel *et al.* 2000, Foster 2001, Pywell *et al.* 2002, Seabloom *et al.* 2003). Although elevated diversity in seed addition experiments may sometimes result from seeding rates that exceed those of natural communities (Moore and Elmendorf 2006), the cumulative rate of 1,550 seeds/m^2 sown in this study is an order of magnitude less than native seed rains of 19,700 seeds/m^2 (Rabinowitz and Rapp 1980) and 15,550 seeds/m^2 (Schott 1993) recorded in remnant tallgrass prairies in Missouri and Kansas respectively. However, the seeding rate in the

present study would still exceed many restoration budgets, illustrating that limited availability and high costs of native forb seed is a major constraint on restoration.

Although interseeding without disturbance can increase native species richness, our findings demonstrate that combining seeding with disturbance can further enhance species richness in grasslands (Pywell *et al.* 2002, Martin *et al.* 2006, Williams *et al.* 2007). Furthermore, the extent to which disturbance improved forb establishment was dependent upon the productivity of each research location. At Nelson, where productivity was significantly lower than other sites, richness of sown species was not significantly increased by disturbance. At McColl, where thatch biomass was significantly less than Prairie Fork, summer burning increased establishment but additional disturbances did not further enhance diversity. Lastly, at Prairie Fork, the most productive site, annual spring burning most effectively suppressed thatch accumulation and significantly increased richness relative to a one-time disturbance of summer burning. These findings illustrate that as productivity and standing biomass increase, the ability of seed addition to enhance local richness declines, and the importance of disturbance generated gaps for colonization and seedling survival increases (Foster 2001, Foster *et al.* 2004).

Our findings generally support the hypothesis that disturbances which most increase light availability enhance forb establishment, though this relationship is most pronounced at sites where light availability is strongly limited by thatch accumulation. While established warm-season grasses are known to inhibit native forb establishment (Kindscher and Tieszen 1998, Copeland *et al.* 2002), multiple regression models indicated that recruitment is more restricted by light suppression from accumulated thatch than by the inhibitive effects of live-biomass from productive warm-season grasses. (Martin *et al.* 2006, MacDougall and Turkington 2007). Litter accumulation reduces germination and seedling establishment as a function of decreased light

availability (Foster and Gross 1998). Given the importance of light as a limiting resource in grassland communities (Collins *et al.* 1998, Camill *et al.* 2004), annual spring burning may be a viable interseeding strategy since this practice very effectively removes thatch and enhances light availability. While spring burning has been shown to increase grass dominance in restorations (Howe 1994a) and remnant prairies (Collins *et al.* 1998), this was not evident at the temporal or spatial scales we examined.

We found partial support for the hypothesis that exotic species establishment would be increased by disturbance, with the caveat that this response was only significant following herbicide application at the one site that had an abundance of exotic species in the surrounding landscape. Although temporary invasion by short-lived exotics is not uncommon following disturbance, the abundance of exotics in plots at Prairie Fork has increased dramatically since initial post-treatment levels (Long and Kindscher 2007) and may have an enduring ecological impact (Cully *et al.* 2003). While cautious application of herbicides can be an important tool for restoration, given the potential for invasion of exotic species in fragmented habitats and the known deleterious effects of glyphosate on amphibian development (Relyea 2005), it would be remiss to recommend non-selective use of broad-spectrum herbicides as interseeding practice.

In this study we found significant differences in native forb community composition among treatments and identified a number of sown species as indicators of specific disturbance regimes at each site. Although the inconsistency of affinities between sown species and disturbance regimes across sites indicates limited predictability of community composition without a more thorough understanding of complex interactions between species functional traits and local environmental conditions, these findings support the mosaic disturbance concept and indicate that application of heterogeneous disturbance regimes within a single restoration site can benefit

forb establishment in restorations using interseeding. Given that species response to disturbance can depend upon localized conditions and native forb seed is a limiting resource for restorations, small-scale sowing experiments could determine which species respond favorably to disturbance regimes prior to implementing novel management at large scales. In less productive grasslands the labor investments of disturbance regimes may provide diminished benefits for forb diversity, but more labor intensive disturbance regimes may optimize the efficacy of interseeding on highly productive sites. Flexible management options also permit practitioners greater ability to adapt to logistical adversities commonly encountered in conservation and restoration practice.

In addition to the benefits of mosaic management for floral diversity, structural heterogeneity increases the wildlife habitat value of grasslands (Fuhlendorf *et al.* 2006, Vogel *et al.* 2007). Increased forb diversity alone can provide habitat for insect species dependent upon native host-plants (Reis *et al.* 2001, Nemec and Bragg 2008), but disturbance induced variation of vegetative structure is important to meet the diverse habitat requirements of grassland fauna, especially declining grassland bird species (Funhlendorf *et al.* 2009, Olechnowski, *et al.* 2009). Grasslands birds such as dickcissels (*Spiza americana*) and Henslow's sparrows (*Ammodramus henslowii*) prefer habitat with dense thatch found in areas that have not been recently disturbed, while grasshopper sparrows (*Ammodramus savannarum*) and bobolinks (*Dolichonyx oryzivorus*) prefer a shallow litter layer such as that created by early spring burns. Species such as greater-prairie chickens (*Tympanuchus cupido*) require a variety habitat structures in close proximity (Delisle and Savidge 1997, Reinking 2005, Fuhlendorf *et al.* 2009), which could be created by implementing mosaic disturbance regimes. Spatial and temporal heterogeneity of disturbance is also important because some management practices can cause direct mortality of wildlife. Burning can increase arthropod abundance creating attractive nesting sites for breeding birds

(Schochat *et al.* 2005), but subsequent mowing during the breeding season can destroy nests and offspring (Harper *et al.* 2007). In addition, variation in burn season is strongly recommended to provide habitat refugia for arthropods and herpetofauna that can be adversely affected by either spring or summer burns depending on species phenology (Harper *et al.* 2007, Vogel *et al.* 2007, Ruthven *et al.* 2008). A diverse mosaic of interseeding management practices should be applied in grassland restorations to concurrently maximize benefits and minimize damage for wildlife.

CONCLUSIONS

The imperiled North American tallgrass prairie biome requires large-scale restoration, yet prairie restorations generally lack the floral and faunal diversity of remnant prairies. We determined that multiple interseeding practices can promote native forb establishment and enhance diversity in warm-season grass plantings. The effects of interseeding practices are contingent upon localized conditions, with greater disturbance intensity necessary to facilitate forb establishment as productivity and light limitation increase. Furthermore, multiple disturbances can promote variable community compositions of sown forbs and create variation in vegetative structure. Mosaic disturbances and interseeding should be conducted to approximate the heterogeneity of historical disturbances and increase floral and faunal diversity in grassland restorations.

Table 1 Chronology of plot delineation, sampling, seed addition, and treatment applications

Time period		Event
Apr	2005	Plots are delineated at each site
Jun	2005 - 2008	Vegetation is sampled in all plots each year
Jul	2005	Herbicide plots sprayed with glyphosate at Praire Fork and Nelson
Aug	2005	All plots are burned except the undisturbed and control plots
Nov	2005	Shallow disking plots are disked
Dec	2005	Seeds are sown in all plots except control plots
Jul	2006	Mowed plots are mowed with rotary mower
Mar	2007 & 2008	Spring burn plots are burned

Table 2 Scientific and common name, 2008 plot frequency of sown species across treatments at each site

		2008 Plot Frequency		
Species	Common Name	Nelson	Prairie Fork	McColl
Achillea millefolium	common yarrow	-	-	-
Amorpha canescens	leadplant	0.07	-	-
Asclepias syriaca	common milkweed	-	-	0.08
Asclepias tuberosa	butterfly milkweed	-	-	-
Baptisia alba	white wild indigo	0.97	0.80	0.88
Chamaecrista fasciculata	partridge pea	0.73	0.70	0.44
Coreopsis palmata	stiff tickseed	0.97	0.43	0.72
Dalea candida	white prairie clover	0.03	-	0.04
Dalea purpurea	purple prairie clover	0.17	0.03	-
Echinacea pallida	pale purple coneflower	0.90	0.20	0.72
Eryngium yuccifolium	button eryngo	0.47	0.57	0.56
Helianthus mollis	ashy sunflower	1.00	0.87	1.00
Heliopsis helianthoides	smooth oxeye	0.97	0.90	0.92
Heuchera richardsonii	Richardson's alumroot	-	-	0.04
Lespedeza capitata	roundhead lespedeza	0.70	0.43	0.64
Lespedeza virginica	slender lespedeza	0.63	0.20	0.68
Liatris aspera	tall blazing star	0.50	0.07	0.28
Liatris pycnostachya	prairie blazing star	0.23	-	0.12
Mimosa quadrivalvis	fourvalve mimosa	0.53	0.10	0.16
Monarda fistulosa	wild bergamot	0.83	0.97	0.96
Oligoneuron rigidum	stiff goldenrod	0.53	0.67	0.60
Penstemon digitalis	talus slope penstemon	0.33	0.20	0.48
Polytaenia nuttallii	Nuttall's prairie parsley	0.33	0.17	0.36
Ratibida pinnata	pinnate prairie coneflower	0.90	0.87	0.92
Rudbeckia hirta	blackeyed Susan	0.97	0.83	0.80
Rudbeckia subtomentosa	sweet coneflower	0.23	0.37	0.32
Salvia azurea	azure blue sage	0.90	0.83	0.92
Solidago nemoralis	gray goldenrod	0.50	0.30	0.68
Solidago speciosa	showy goldenrod	0.23	-	0.32
Symphyotrichum laeve	smooth blue aster	-	-	0.04
Symphyotrichum novae-angliae	New England aster	0.83	0.97	1.00
Symphyotrichum oolentangiense	skyblue aster	-	-	-
Verbena hastata	swamp verbena	-	0.10	0.08
Verbena stricta	hoary verbena	0.30	0.20	0.20
Vernonia baldwinii	Baldwin's ironweed	0.77	0.83	0.64
Veronicastrum virginicum	Culver's root	-	-	-
Zizia aurea	golden zizia	0.63	1.00	0.80

Table 3 Results of 2-way ANOVA tests for effects of site, treatment, and site x treatment intereactions

Response Variable	Site	Treatment	Site x Treatment
Light Availability (%PAR)	$F = 10.5_{2,68}$ $p < 0.001$	$F = 16.1_{5,68}$ $p < 0.001$	*n.s.*
Grass Biomass (g)	$F = 13.3_{2,68}$ $p < 0.001$	$F = 13.9_{5,68}$ $p < 0.001$	$F = 2.7_{9,68}$ $p < 0.01$
Thatch Biomass (g)	$F = 40.2_{2,56}$ $p < 0.001$	$F = 15.6_{4,56}$ $p < 0.001$	$F = 4.6_{7,56}$ $p < 0.001$
Sown Species			
Richness	$F = 14.5_{2,68}$ $p < 0.001$	$F = 12.3_{5,68}$ $p < 0.001$	$F = 2.8_{9,68}$ $p < 0.01$
Evenness	$F = 4.82_{2,68}$ $p = 0.01$	*n.s.*	$F = 2.9_{9,68}$ $p < 0.01$
Diversity	$F = 18.4_{2,68}$ $p < 0.001$	$F = 14.5_{5,68}$ $p < 0.001$	$F = 4.1_{9,68}$ $p < 0.001$
Density	$F = 12.3_{2,68}$ $p < 0.001$	$F = 14.8_{5,68}$ $p < 0.001$	*n.s.*
% Cover	$F = 8.5_{2,68}$ $p < 0.001$	$F = 10.1_{5,68}$ $p < 0.001$	*n.s.*
Biomass (g)	$F = 19.8_{2,68}$ $p < 0.001$	$F = 6.3_{5,68}$ $p < 0.01$	*n.s.*
Total Native Species			
Richness	$F = 18.3_{2,72}$ $p < 0.001$	$F = 16.7_{6,72}$ $p < 0.001$	*n.s.*
Diversity	$F = 27.5_{2,72}$ $p < 0.001$	$F = 13.9_{6,72}$ $p < 0.001$	$F = 2.2_{11,68}$ $p < 0.05$
Exotic Species			
Richness	$F = 39.2_{2,68}$ $p < 0.001$	$F = 5.6_{5,68}$ $p < 0.001$	*n.s.*
Density	$F = 43.9_{2,68}$ $p < 0.001$	$F = 37.4_{5,68}$ $p < 0.001$	$F = 16.5_{9,68}$ $p < 0.001$
% Cover	$F = 57.5_{2,68}$ $p < 0.001$	$F = 19.4_{5,68}$ $p < 0.001$	$F = 8.5_{9,68}$ $p < 0.001$

Table 4 Stepwise multiple regression models for determining which explanatory variables are the stongest determinants of sown and exotic species richness and density

	Predictor	Parameter Estimate	SE	Partial Correlation	*p*
Sown Species Richness					
	Thatch Biomass	-0.020	0.004	-0.452	1.6E-05
	Light Penetration	7.974	2.509	0.331	2.1E-03
Model : df = 2, 82 ; F = 30.66, r^2 = 0.428; P =1.1E-10					
Sown Species Density					
	Light Penetration	97.510	21.095	0.455	1.4E-05
	Thatch Biomass	-0.073	0.0364	-0.217	4.8E-02
Model : df = 2, 82 ; F = 23.25, r^2 = 0.362; P =1.0E-08					
Exotic Species Richness					
	Light Penetration	1.945	0.550	0.362	6.6E-04
Model: df =1, 83 ; F = 6.89, r^2 = 0.131; P =6.6E-04					
Exotic Species Density					
	Grass Biomass	-82.342	17.048	-0.468	6.2E-06
Model: df =1, 83 ; F = 23.33, r^2 = 0.219; P =6.2E-06					

Table 5 Results of Indicator Species Analysis. Group indicates treatments in which each species exhibited maximal abundance. Indicator values (IV) are measures (0 to 100) of the fidelity of species occurrence with a particular group (Dufrene & Legendre 1997). Probability values (Prob.) refer to Monte Carlo tests. Bold values indicate significant indicator values ($p < 0.05$).

	Nelson			**Prairie Fork**			**McColl**		
Species	**Group**	**IV**	**Prob.**	**Group**	**IV**	**Prob.**	**Group**	**IV**	**Prob.**
Achillea millefolium	-	-	-	-	-	-	-	-	-
Amorpha canescens	Undist	10	1.00	Disking	20	1.00	-	-	-
Asclepias syriaca	-	-	-	-	-	-	-	-	-
Asclepias tuberosa	-	-	-	-	-	-	-	-	-
Baptisia alba	**Disking**	**39**	**0.00**	SprBurn	26	0.24	Mowing	34	0.21
Chamaecrista fasciculata	SprBurn	14	0.96	Glyphos	17	0.63	Disking	15	1.00
Coreopsis palmata	Glyphos	30	0.15	Disking	13	0.89	Disking	25	0.49
Dalea candida	Mowing	20	1.00	-	-	-	SprBurn	20	1.00
Dalea purpurea	Glyphos	12	1.00	-	-	-	-	-	-
Echinacea pallida	Mowing	26	0.14	SprBurn	30	0.16	Disking	28	0.46
Eryngium yuccifolium	Glyphos	16	0.66	**Glyphos**	**36**	**0.07**	Mowing	20	0.60
Helianthus mollis	Disking	24	0.19	Glyphos	27	0.30	SprBurn	23	0.72
Heliopsis helianthoides	Disking	30	0.13	SumBurn	18	0.67	Disking	28	0.52
Heuchera richardsonii	-	-	-	-	-	-	Mowing	20	1.00
Lespedeza capitata	Mowing	28	0.19	Glyphos	16	0.67	SumBurn	20	0.52
Lespedeza virginica	Mowing	28	0.23	SumBurn	10	1.00	SumBurn	38	0.11
Liatris aspera	Glyphos	20	0.82	SprBurn	20	1.00	Mowing	20	0.76
Liatris pycnostachya	Disking	30	0.25	-	-	-	Mowing	20	1.00
Mimosa quadrivalvis	Glyphos	12	0.96	-	-	-	Disking	27	0.21
Monarda fistulosa	Undist	29	0.32	**Glyphos**	**44**	**0.04**	SumBurn	24	0.71
Oligoneuron rigidum	Glyphos	29	0.16	**Mowing**	**40**	**0.04**	SumBurn	24	0.49
Penstemon digitalis	**Undist**	**53**	**0.01**	Mowing	7	1.00	Disking	25	0.36
Polytaenia nuttallii	Undist	16	0.88	Mowing	10	1.00	Mowing	20	0.61
Ratibida pinnata	**Glyphos**	**33**	**0.05**	Glyphos	21	0.71	**SumBurn**	**33**	**0.07**
Rudbeckia hirta	Glyphos	30	0.27	SprBurn	27	0.50	SprBurn	38	0.19
Rudbeckia subtomentosa	**Glyphos**	**60**	**0.02**	Disking	6	0.99	-	-	-
Salvia azurea	**Glyphos**	**35**	**0.00**	SprBurn	18	0.86	**SprBurn**	**34**	**0.05**
Solidago nemoralis	Glyphos	42	0.17	Glyphos	20	0.51	**SumBurn**	**56**	**0.01**
Solidago speciosa	Glyphos	13	0.87	-	-	-	SumBurn	7	1.00
Symphyotrichum laeve	-	-	-	-	-	-	-	-	-
Symphyotrichum novae-angliae	**Glyphos**	**46**	**0.00**	Mowing	31	0.13	SumBurn	34	0.11
Symphyotrichum oolentangiense	-	-	-	-	-	-	-	-	-
Verbena hastata	-	-	-	Glyphos	20	1.00	SumBurn	16	0.46
Verbena stricta	Disking	20	0.39	SprBurn	10	1.00	Mowing	20	1.00
Vernonia baldwinii	Mowing	11	1.00	Disking	36	0.24	SprBurn	19	0.59
Veronicastrum virginicum	-	-	-	-	-	-	-	-	-
Zizia aurea	Undist	20	0.61	Mowing	25	0.59	Undist	29	0.32

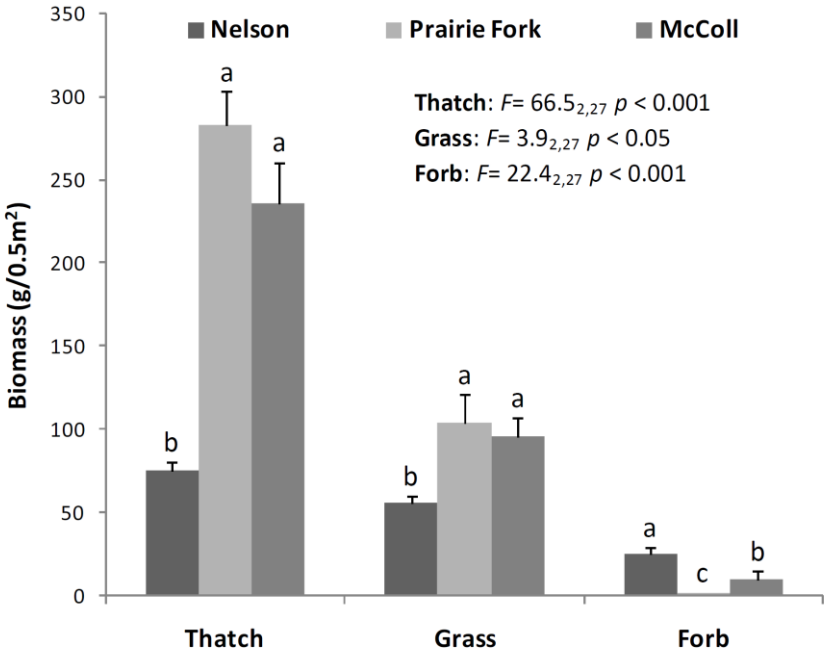

Figure 1 Mean baseline values of biomass, recorded as the average dry weight (g) per 0.25m^2, for thatch, grasses, and forbs at each research location in 2005. Results are shown for ANOVA test examining differences among sites for each biomass type, and sites without a common letter are significantly different ($p < 0.05$).

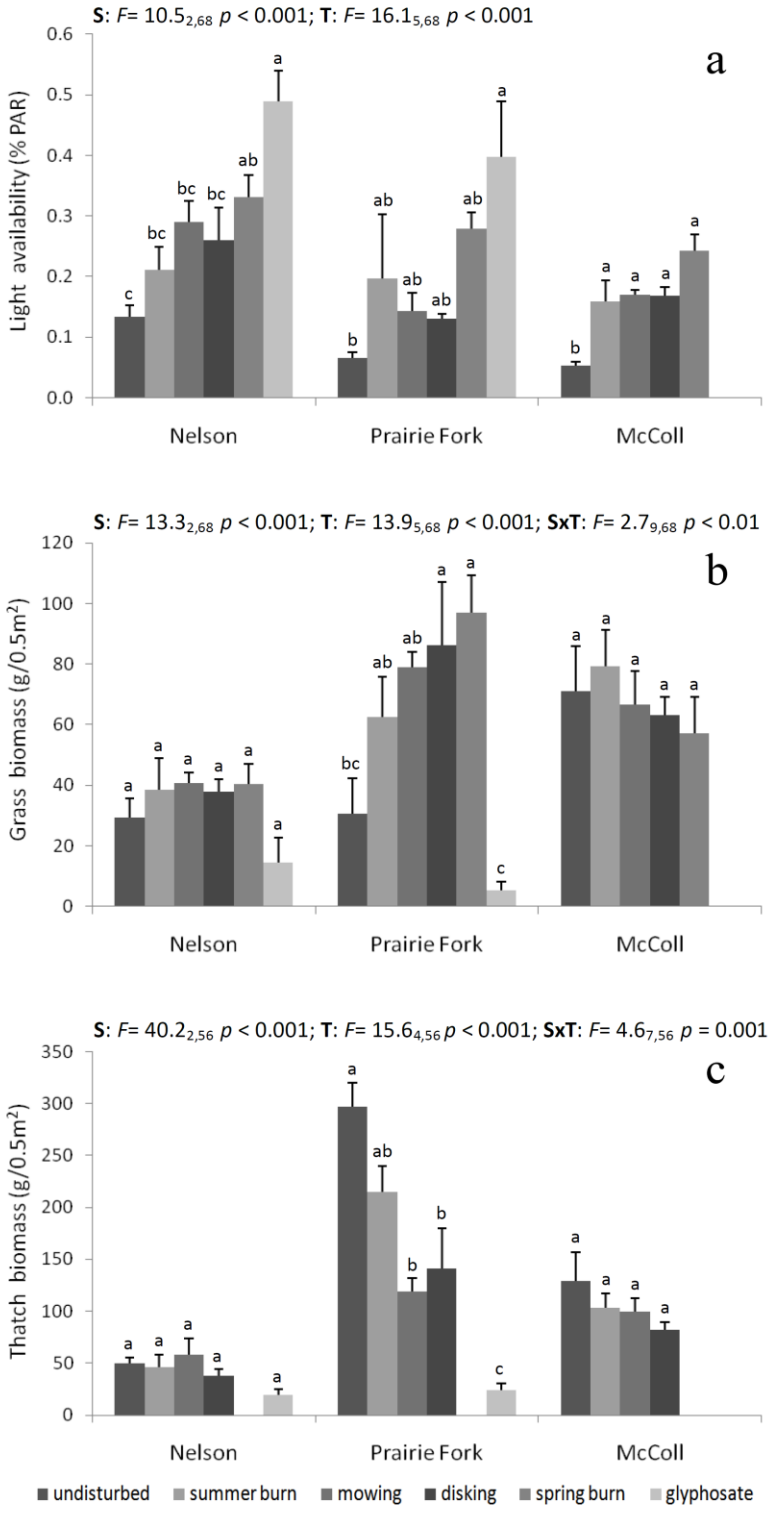

Figure 2 Mean percent light availability (a), grass biomass (b), and thatch biomass (c) per treatment (+/-1 SE). Significant site (S), treatment (T), and site x treatment (SxT) interactions are shown for each variable. Significant differences ($p < 0.05$) in pairwise comparisons of treatments within sites are denoted by absence of a common letter.

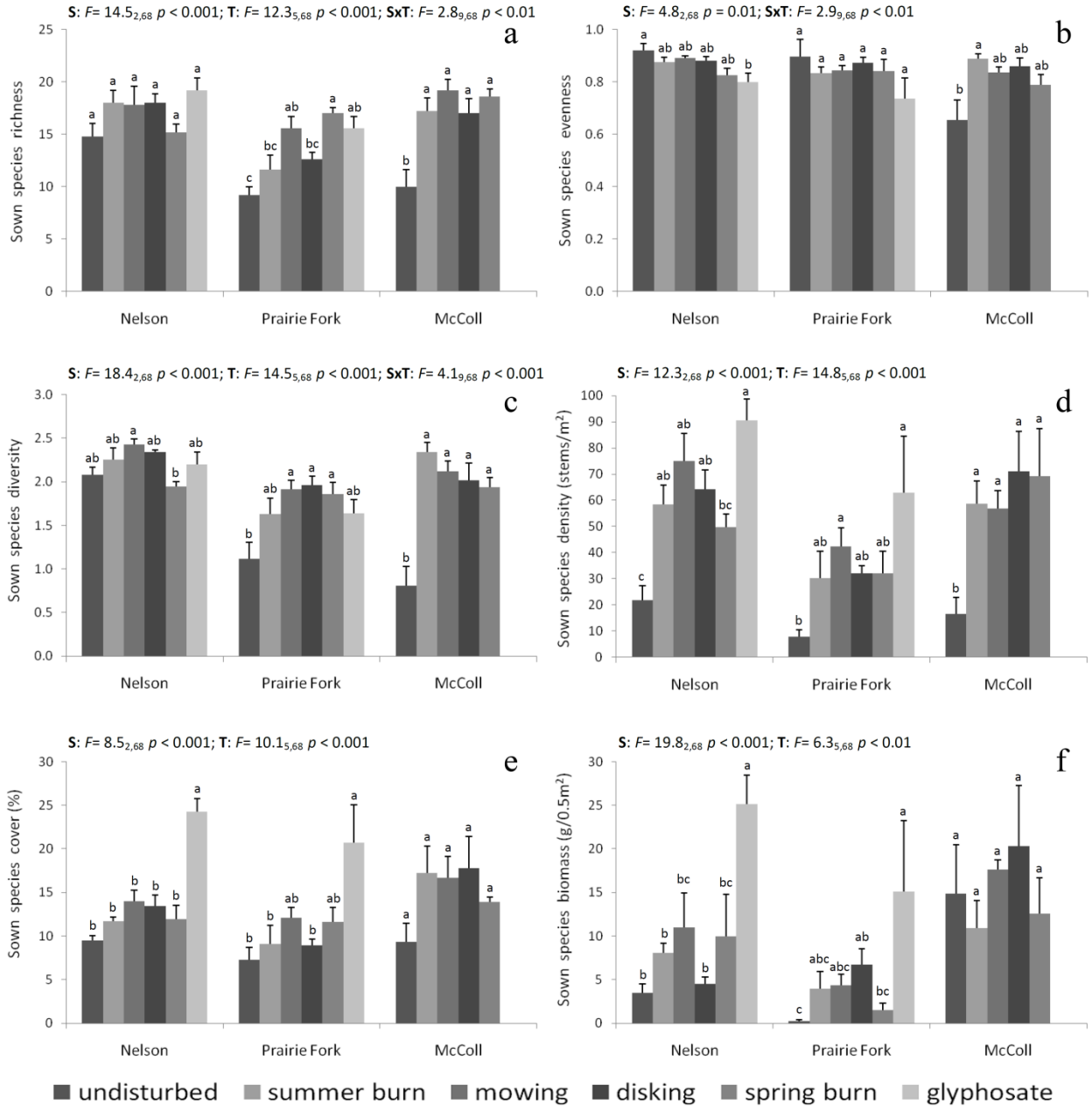

Figure 3 Mean richness (a), evenness (b), diversity (c), density (d), cover (e), and biomass (f) of sown species per treatment (+/-1 SE). Significant site (S), treatment (T), and site x treatment (SxT) interactions are shown for each variable. Significant differences ($p < 0.05$) in pairwise comparisons of treatments each site are denoted by the absence of a common letter.

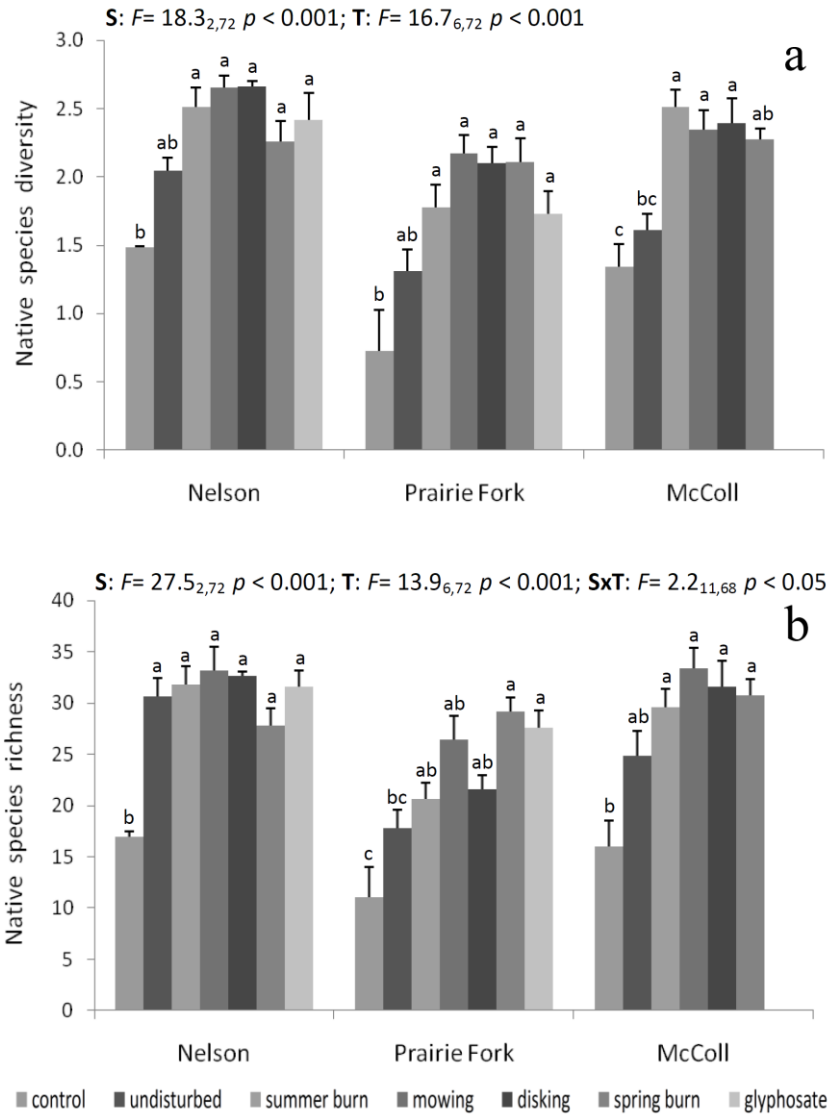

Figure 4 Mean Shannon diversity (a) and richness (b) of native species per treatment (+/-1 SE). Significant site (S), treatment (T), and site x treatment (SxT) interactions are shown for each variable. Significant differences ($p < 0.05$) in pairwise comparisons of treatments within each site are denoted by the absence of a common letter.

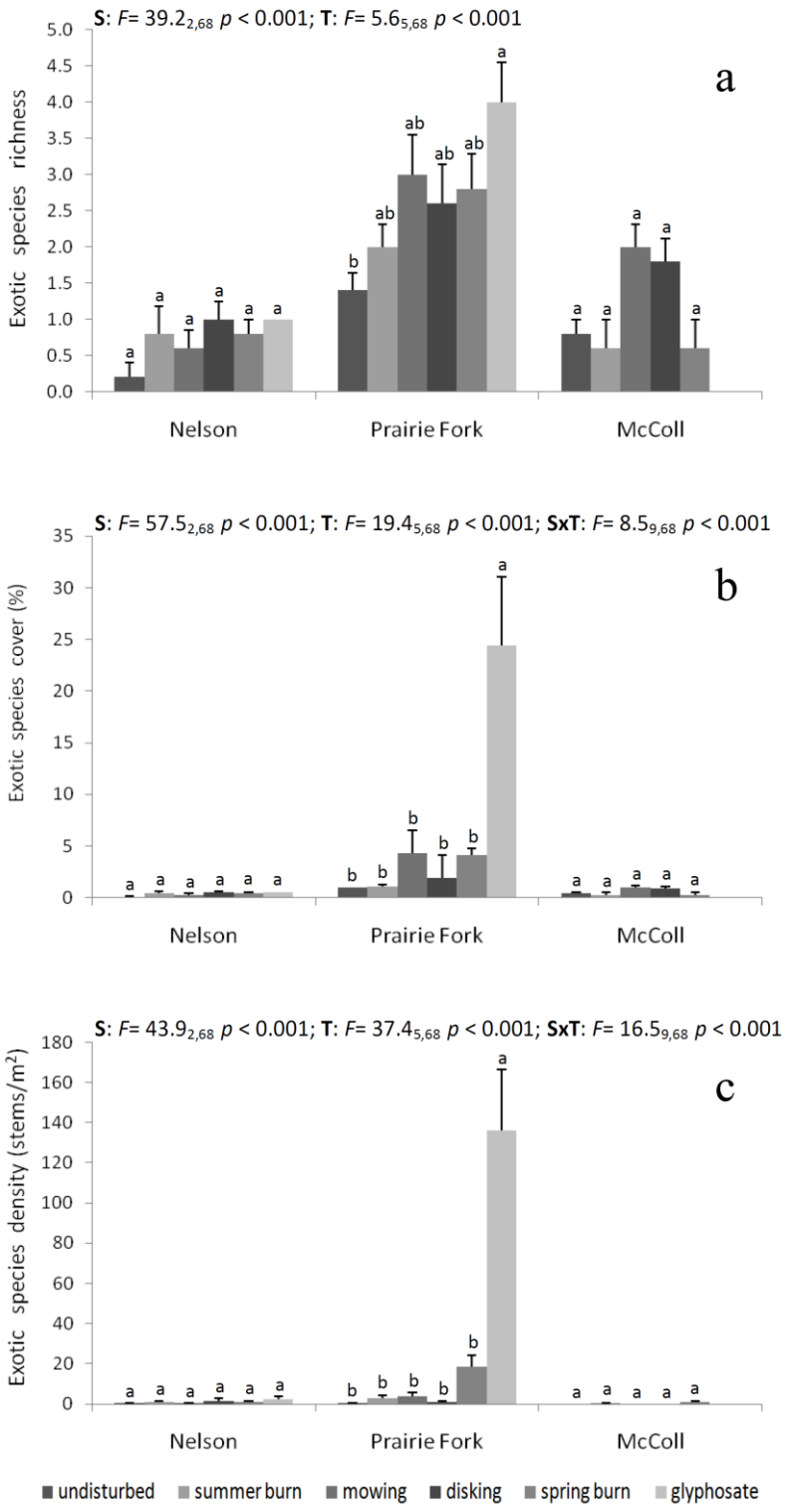

Figure 5 Mean richness (a), cover (b), and stem density (c) of exotic species per treatment (+/-1 SE). Significant site (S), treatment (T), and site x treatment (SxT) interactions are shown for each variable. Significant differences ($p < 0.05$) in pairwise comparisons of treatments within each site are denoted by the absence of a common letter.

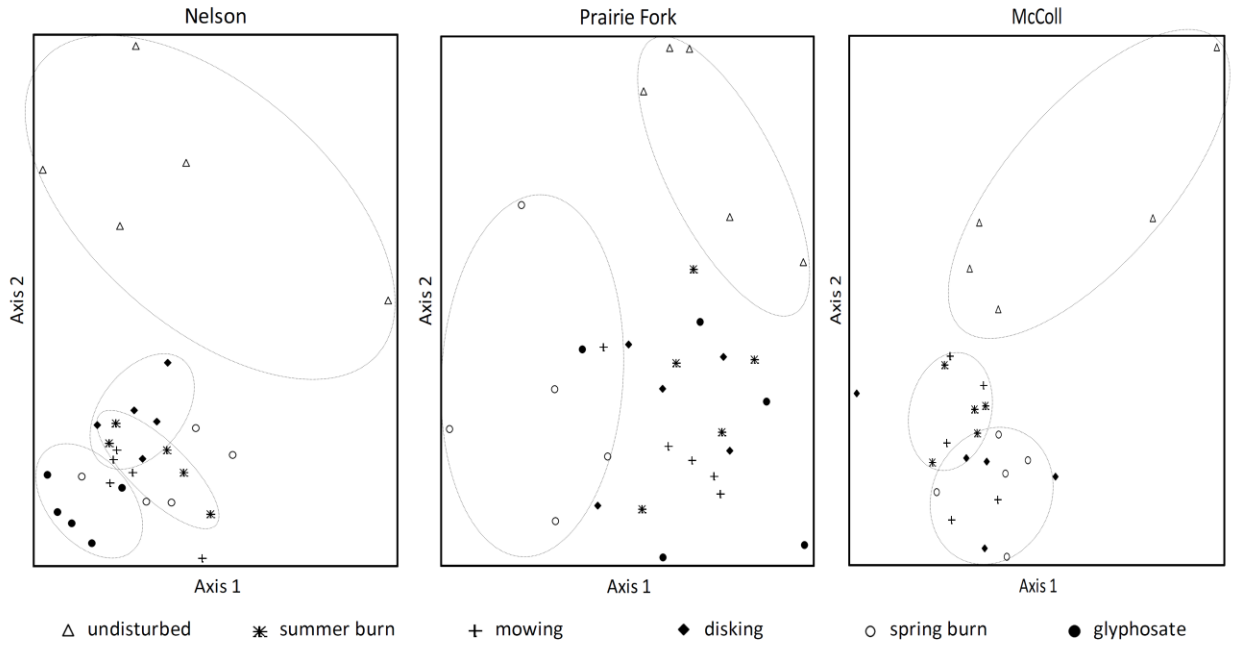

Figure 6 Ordination biplots illustrating results of Non-metric Multidimensional Scaling and treatment identity for individual research plots. Envelopes are shown for treatments which had significantly different composition of sown species in PERMANOVA tests.

GENERAL CONCLUSIONS

The collective results of this dissertation serve to further our understanding of the ecological intricacies of recruitment dynamics in tallgrass prairies. I have examined how stochasticity, plant traits, and multiple disturbance regimes can each affect the outcome of colonization events in restored grasslands, exemplifying how ecological experiments can address fundamental issues of basic ecology with applications for restoration and conservation practice. Employing principles of community ecology to interpret recruitment processes holds great promise for enhancing the diversity of tallgrass prairie restorations.

The findings of my first chapter provide further support for the emergent perspective that both niche-based and stochastic forces collectively structure ecological communities. My results illustrate how propagule pressure and disturbance can moderate the relative influence of stochasticity on sown species assemblages. By manipulating both propagule pressure and disturbance in a species-poor native grassland, I was able to demonstrate how infrequent recruitment due to dispersal limitations and low resource availability can impose a stochastic filter on the composition of sown plant communities. Analyses of the compositional dissimilarity of sown species within and among treatment levels confirmed that higher recruitment rates in response to propagule pressure and disturbance can overwhelm stochastic effects on the composition of species assemblages at early recruitment stages.

It is possible that stochasticity was moderated by increased dispersal due to the probabilistic chance that communities with greater stem densities would contain a larger proportion of species from the regional pool of potential colonists, which would be consistent with the assertions of neutral theory. However, greater propagule pressure also revealed deterministic species-sorting

dynamics, which produced divergent compositions associated with the specific environmental conditions of each disturbance regime. These observed species-sorting dynamics rely upon niche-differentiation among colonists with respect to environmental conditions for recruitment, which is incongruent with the neutral assumption of ecological equivalence. Amplifying the stem density of sown species may have increased within-treatment compositional similarity by concurrently intensifying interactions among colonists and raising the probability that species with asymmetric competitive abilities would compete for resources at highly localized spatial scales. High propagule pressure magnified divergence of species compositions among treatments while also increasing the significance of species affinities for specific disturbance treatments.

Experimental manipulation of dispersal rates and disturbance intensity provides insights for basic ecology by revealing processes that may express a more subtle influence on stochasticity in natural communities. While dispersal and immigration do not naturally occur in such finite gradients as those imposed by seed-addition experiments, variation in patch-connectivity encountered in fragmented natural communities can result in considerable disparity in the extent to which dispersal limitation affects local species composition. Accordingly, the results of my seed addition study indicate that stochasticity should have a more prominent effect on species assemblages in highly fragmented landscapes with strong dispersal limitations. Future work is needed to examine the interaction between fragmentation, dispersal limitation, and compositional stochasticity in natural systems in which propagule pressure is the result of natural dispersal.

Furthermore, a greater understanding of how propagule pressure and disturbance moderate the stochasticity of recruitment events has applied implications for ecological restoration. Low species turnover among patches at small spatial scales may decrease diversity at larger scales (Chase 2003), indicating that heightened competitive interactions following high recruitment

density may constrain landscape scale diversity in the absence of environmental heterogeneity. In contrast, species-sorting patterns suggest that both diversity and within-patch predictability of community composition in large-scale restorations could be maximized when heterogeneous disturbances are prescribed concurrently with high propagule pressure. Obviously, there is great interest among practitioners in determining optimum seeding rates for restorations (Weber 1999, Burton et al. 2006, Sheley and Half 2006). While insufficient seeding density will hinder a restoration project, excessive seeding rates waste limited economic resources (Stevenson et al. 1995). Furthermore, my findings indicate that, without substantial environmental heterogeneity, excessive seeding rates may inhibit large-scale diversity due to the uniform dominance of competitively superior species (Weber 1999, Burton et al. 2006). This constraint on diversity is anticipated because greater compositional similarity among homogenous patches decreases β-diversity, which inherently constrains α-diversity at large scales.

Having shown that seed addition can promote relatively predictable patterns of community composition, it is of considerable interest to examine which traits may determine a species' potential for successful recruitment. In my second chapter I compiled recruitment data for 190 species collectively sown in 54 restoration studies in order to identify persistent relationships between plant traits and recruitment success in grasslands. My analyses of 10 plant traits demonstrated that increased recruitment potential was associated with flowering during mid to late summer, long flowering duration, intermediate height, intermediate seed mass, and clonality. It was of particular interest that species with intermediate seed mass had the greatest recruitment potential despite expectations that large-seeded species would exhibit consistently high recruitment. Given the variance in recruitment success associated with particular trait values, it cannot be asserted that possession of any given trait assures successful recruitment. Rather,

advantageous traits set a high upper bound on recruitment potential, while disadvantageous traits may severely restrict recruitment. Many traits vary independently and recruitment potential is greatest when multiple beneficial traits such as seed mass and height act in concert. However, recruitment can be severely limited by syndromes of disadvantageous traits such as small seed mass, short height, early flowering time, and short flowering duration.

It is to be expected that the predictive statistical power of these findings would be limited given that the compiled studies represent a diverse amalgamation of geographic locations, soil conditions, precipitation levels, and management histories. Naturally, any of these factors could affect species recruitment, as demonstrated by the potential for divergence among the species compositions associated with disturbance regimes in the first chapter. However, this study has illuminated general trait-based recruitment patterns that emerge despite statistical noise caused by the varied environmental contexts of these studies from throughout the tallgrass region. These findings have established a foundation for future research that is needed to further integrate trait-based knowledge into management practice. A greater understanding of how plant traits influence recruitment holds the potential to advance our understanding of community assembly and to facilitate the conservation and restoration of degraded ecosystems.

In my third chapter I examined the effect of multiple disturbance regimes on forb recruitment in species-poor restorations at three Midwestern research areas and evaluated the potential for mosaic disturbance management to increase floral and structural heterogeneity. Methods of enhancing forb diversity in established warm-season grasslands had been poorly investigated despite the limited diversity attained by most tallgrass restorations. I found that sowing native forbs increased native species richness even without disturbance, though disturbances generally enhanced both the richness and abundance of established sown species. These results indicate

that local richness was limited both by propagule availability and free microsites for recruitment. Light availability was a strong predictor of recruitment, and the benefit of increased disturbance intensity was contingent upon the extent to which productivity limited light availability at each location. At the Missouri field site where exotic species were abundant in the surrounding landscape, initial broad-spectrum herbicide application promoted invasion. These findings jointly suggest that greater diversity can be achieved through forb enrichment of existing tallgrass restorations if adequate seeding rates of a diverse forb mixture are sown in conjunction with site-appropriate disturbance regimes.

While no particular disturbance regime led to markedly superior establishment of sown species, we found significant differences among the native forb community compositions and habitat structure associated with treatments. Given the variable habitat needs of declining grassland bird species, it would be beneficial for restorations to incorporate mosaic management practices to create proximate patches with diverse vegetative structures. Mosaic disturbances and diverse forb interseeding should be conducted in concert within restoration sites to approximate the heterogeneity of historical disturbance patterns and to enhance the floral diversity and wildlife habitat value of restored grasslands.

Synthesis, Assessment, and Implications for Practice

Given that each of these dissertation chapters shares the expressed objective of facilitating the restoration of tallgrass prairies, it is necessary to address how the collective findings of these studies can be applied to enhance restoration practice and, furthermore, what insights this body of work provides regarding the feasibility of restoring this imperiled grassland biome. In order to address these issues, one must have a clear sense of what the objectives of ecological restoration are and how the success of restorations can be appropriately assessed. The Society for Ecological

Restoration International (SERI 2004) defines ecological restoration as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed." This broad definition allows considerable flexibility, as the objectives of restoration projects are contingent upon how 'recovery' is interpreted. While multiple criteria can be used to evaluate recovery at various stages on the trajectory between degraded and restored ecosystems, the most prominent criterion for assessing the success of a restoration is that "the restored ecosystem contains a characteristic assemblage of the species that occur in the reference ecosystem and that provide appropriate community structure" (SERI 2004).

For the North American tallgrass prairie, the desired endpoint or "references" for restoration is to approximate the historical condition of that ecosystem as it existed prior to Euro-American settlement. While it is certain that no reference community in the tallgrass region has been completely unaltered from its historical condition, remnant prairies that have never been tilled or excessively grazed, such as haymeadowprairies in eastern Kansas, are the most suitable reference by which to measure the success of my restoration experiments in an applied context. Jog et al. (2006) conducted surveys of warm-season CRP fields and remnant hay meadow prairies (n=20) in eastern Kansas, during which they gathered data on species richness in both $1m^2$ plots and $20m^2$ plots throughout each site. While formal statistical comparison of data from the surveys by Jog et al. (2006) and data from the restoration field experiments conducted in this dissertation is not justified given the very disparate sample sizes of these studies, their surveys do provide an accessible benchmark for assessing the success of my experimental restorations.

As reported in the third chapter, the pre-treatment native species richness at Nelson, Prairie Fork, and McColl was very characteristic of the low diversity reported for warm-season CRP fields by Jog et al. (2006). By the final sampling period of my restoration experiments in 2008,

native richness per $1m^2$ at the Nelson site was nearly equivalent to that of native hay meadows for the summer burn, mowing, disking, and glyphosate treatments conducted in chapter 3 (See Fig 1 below), all of which were sown at the same density of 1,550 seeds/m^2 that was used for the mid propagule pressure treatments in Chapter 1. The mid and high propagule pressure treatments in Chapter 1 also obtained native richness at the $1m^2$ scale that was roughly equivalent to that reported from remnant native hay meadows, though low propagule pressure treatments resulted in substantially lower small-scale richness (Fig 1). While the disturbance and seed addition treatments conducted at Prairie Fork and McColl dramatically enhanced richness relative to their pre-treatment levels, native richness at the $1m^2$ scale was still substantially lower than reference prairie communities (Fig 1). These comparisons indicate that multiple interseeding practices are capable of successfully restoring small scale richness, provided that a sufficient quantity and diversity of native seed is available, and that recruitment is not inhibited by the high productivity encountered at sites such as the Prairie Fork and McColl research areas.

Although successful restoration of native richness at the $1m^2$ scale is encouraging, additional metrics are needed to evaluate restoration success. While the surveys by Jog et al. (2006) did not record abundance and cannot assess vegetative characteristics such as evenness and diversity, presence data is well suited for Floristic Quality Assessment (FQA; Wilhelm 1977, Swink and Wilhelm 1979). FQA is a standardized tool used to estimate the floristic and ecological quality of natural areas based on vascular plant surveys (Taft et al. 1997, Freeman and Morse 2002), and is frequently used to evaluate the efficacy of restoration in a wide variety of natural communities. The FQA method is based on calculating an average coefficient of conservatism (C) and a Floristic Quality Index (FQI) for a site. A coefficient of conservatism is an integer from 0–10 that is assigned to each native plant species in a given geographic region. Species with high

conservatism values (7–10) only occur naturally in high quality habitats such as remnant prairies, whereas species with low values (0-3) are able to persist through human disturbance or recolonize disturbed sites (Swink & Wilhelm 1979). The mean C of all species present is multiplied by the square root of the total number of species ($\sqrt{N}$) inventoried in a site (FQI = mean C $\times$ $\sqrt{N}$) to calculate a FQI, which can then be compared to the FQI of reference communities to assess the success of ecological restoration projects. In order to more closely approximate the sampling area used by Jog et al. (2006) for FQA, I calculated FQI values by combining presence data for all disturbance treatments at each site. This approach also serves to measure the floristic quality produced by mosaic interseeding practices at each research area. Consistent with patterns of native species richness, FQI values at the Nelson area very closely approximated the mean FQI reported by Jog et al. (2006) for native hay meadows, while both the Prairie Fork and McColl sites greatly improved relative to pre-treatment conditions but did not approximate the floristic quality of the reference remnant communities (see Fig 2 below).

While metrics such as small-scale native richness and FQI that can be readily quantified are useful for evaluating the progress of restorations, there are numerous other qualities such as vegetative structure, productivity, and the collective identity, abundance, and distribution of native and exotic species that would require exhaustive data collection to properly quantify. However, these same community characteristics can be rapidly assessed by any skilled botanist familiar with high quality reference communities. Based on my extensive experience conducting floristic surveys of remnant native prairies and my exhaustive familiarity with the restoration experiments conducted in this dissertation, I have formed some general conclusions regarding the viability of tallgrass prairie restoration and interseeding practices. Restoration of highly productive sites such as Prairie Fork and McColl will require very intensive long-term

management with prescribed disturbances and interseeding in order to more closely approximate reference communities, but may never be fully restored to a historical condition. This is primarily due to the inhibitive effects of the native-warm season grass species that have been established there. Although the origins of the seed used for these plantings during the mid-1980s could not be confirmed, the vegetative structure and prolific productivity of the warm-season grasses at these sights strongly suggests that they are not local ecotypes, but rather cultivars selected for high productivity. Such cultivar grass species may be appropriate for livestock forage and biofuels, but their dominance in warm-season grass plantings can strongly inhibit the establishment of a diverse native forb community. Although restoration practitioners are increasingly aware of the importance of using local ecotype grasses, the use of these aggressive warm-season grass cultivars in CRP plantings is unfortunately still standard practice.

It is important to recognize that the experiments conducted in this dissertation portray initial recruitment and still represent the early stages of a successional restoration trajectory. The species composition of restored ecosystems continues to evolve with changing environmental conditions (SERI 2004). Continued management and seeding will continue to improve the restorations at Prairie Fork and McColl, though it is uncertain whether the inhibitory effect of the dominant grasses will ever permit these communities to reach the objective of approximating the composition of native remnant prairies. Despite these tempered expectations, restorations such as these can still provide important ecosystem, conservation, educational, and aesthetic values, and will benefit from continued interseeding and the prescription of mosaic disturbance regimes.

Unlike those of the Prairie Fork and McColl sites, the native warm season grasses at the Nelson area appear to be locally ecotypes. This site was planted to native grasses in 1957 and the present structure and productivity of the native grasses appears equivalent to a nearby remnant,

Rockefeller Prairie, which serves a reference for local restoration objectives. Comparisons with native prairies surveyed by Jog et al. (2006) indicate that several of the experimental restoration practices explored in this dissertation are capable of replicating the small scale richness and floristic quality of remnant prairies. Given that only 37 species were sown in these experiments due to limited commercial availability of seed, these seeding efforts cannot be expected to replicate the large scale diversity of native remnants that may contain in excess of 100 native species in an area of only several acres (Kindscher et al. 2009). However, I believe that if seed could be obtained locally for species representing the full complement of remnant diversity and sown in conjunction with mosaic disturbances, within a decade the Nelson area could obtain such diversity that a skilled botanist would have difficulty distinguishing it from a high quality remnant. As suggested by the propagule pressure experiment of Chapter 1, such seeding should be done at moderate rates in order to increase the compositional heterogeneity of recruitment. Furthermore, sowing practices should account for disparate competitive abilities by only sowing highly competitive species with traits such as clonality in discrete patches across the landscape.

While it is encouraging to suggest that species-poor stands of local-ecotype native grasses such as Nelson are capable of being fully restored, attaining such complete restoration is dependent upon acquiring seed for many species that occur in low abundance even on remnants. Unfortunately, seed for many native species is either commercially unavailable or prohibitively expensive. Local collection of all desirable species is ideal if there are nearby populations from which to collect, but a comprehensive collection effort requires far more employee or volunteer hours than are available for most restoration efforts. As a result, the unavailability of large quantities of affordable, locally adapted seed for a high diversity of species is a major constraint on the ability to fully restore the native diversity found in remnant tallgrass prairies.

Trait-based analyses in the second chapter identified plant traits that may substantially limit recruitment for certain species even if adequate amounts of their seed can be obtained. However, further work is needed before trait-based knowledge can be comprehensively integrated into the restoration process. This is partially because local environmental conditions can strongly impact trait relationships, as demonstrated by the indicator species analysis conducted in the first and third chapters. In the third chapter, none of the significant associations between sown species and disturbance treatments were consistent across the three experimental sites, suggesting that strong effects of local conditions on species establishment could alter trait-based recruitment patterns. Evaluation of the relationships between the traits examined in chapter 2 and the species which were significant indicators of disturbance treatments at the Nelson area in Chapter 1 did not reveal any convincing trait-based justification for the observed affinities between sown species and treatments. However, these associations between indicator species and particular disturbance treatments were readily observable in the field, suggesting that the Indicator Species Analysis (ISA) results in Chapter 1 were not merely statistical aberrations. It is possible that more difficult to quantify functional traits such as shade tolerance, relative growth rate, photosynthetic efficiency, and species nutrient requirements could provide a sound ecological justification for the observed affinities between species and disturbance treatments if environmental qualities such as light availability, soil moisture, and soil nutrient levels were also meticulously quantified. Accordingly, the application of trait-based knowledge to restoration practice may be greatly facilitated by the completion of the comprehensive 'traitnet' database for functional traits of the North American Flora.

While ecological experiments can make substantial contributions to the restoration of plant communities, the implementation of formal research into applied restoration practice ultimately

requires translation by practitioners with intimate knowledge of local environmental conditions. This dissertation has identified multiple constraints on restored diversity and suggested directions for management and future research that will hopefully contribute to the restoration of the imperiled tallgrass ecosystem. Collectively, my three dissertation chapters examined various facets of recruitment dynamics in restored tallgrass prairies. These studies demonstrated that the diversity and composition of recruitment events is affected by many factors, including propagule pressure, the form and intensity of disturbance regimes, the traits of sown species, and the environmental characteristics of the sites into which species are sown. Recruitment is a vital process for coexistence in plant communities, and examination of recruitment patterns in the experimental context of restored grasslands provides an ideal framework for addressing basic ecological questions with direct applications for ecological restoration.

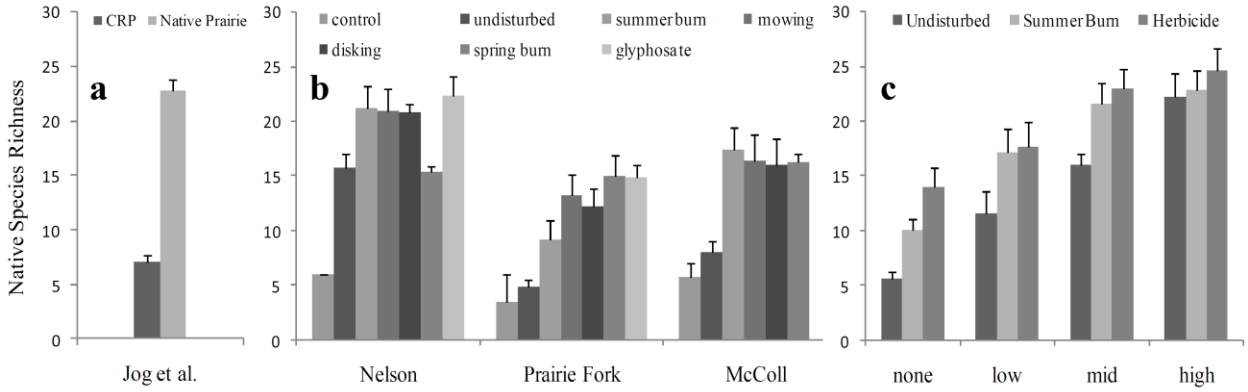

Fig 1 The mean native species richness per $1m^2$ (+1 SE) recorded in (**a**) surveys of warm-season CRP plantings and native tallgrass prairies in Kansas by Jog et al. (2006), compared with the total native species richness per $1m^2$ (+1 SE) recorded in the final sampling period of the (**b**) forb interseeding study conducted in chapter 3 and the (**c**) propagule pressure and disturbance study conducted in chapter 1.

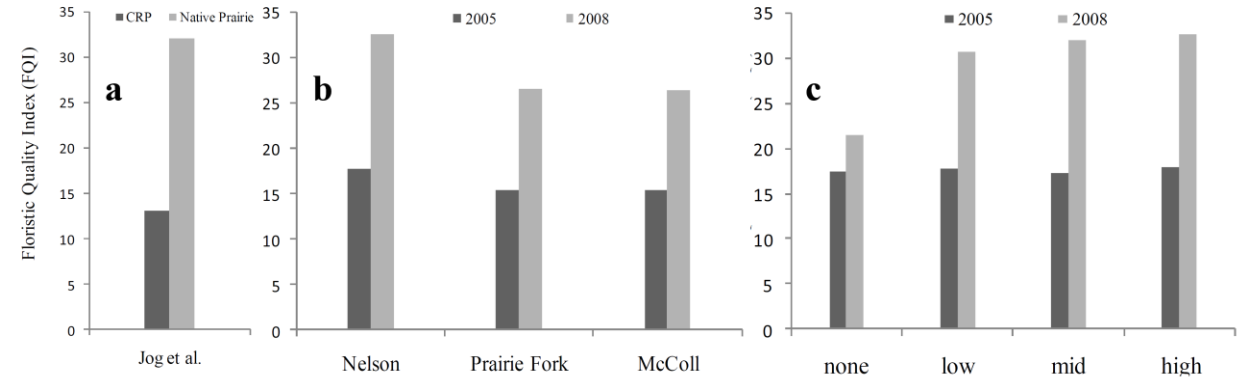

Fig 2 Floristic Quality index (FQI) recorded in (**a**) surveys of warm-season CRP plantings and native tallgrass prairies in Kansas by Jog et al. (2006), compared with FQI values calculated based on presence data from the final sampling period of the (**b**) forb interseeding study conducted in chapter 3 and the (**c**) propagule pressure and disturbance study conducted in chapter 1.

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